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BIOCHARACTERS AS SEPARABLE UNITS OF ORGANIC STRUCTURE

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INTRODUCTION

As to the term "character," in the commonly accepted sense of zoology and botany, it has long been known that different characters, large and small, exhibit different rates of evolution and are in this sense "separable" or "independent," while in another sense it has long been known that every character of an organism is correlated or coordinated with every other character in function and adaptation. Our general knowledge of character separability (for the want of a better English term) has been more than confirmed by researches based upon the great discovery of Mendel, namely, that many large as well as minute characters which are closely associated or even blended in the adult organism are very sharply separated from each other in the germ plasm, in such a manner that they may entirely appear or disappear in the crossing, or hybridization of species, subspecies, varieties, races, no less than of individuals. The theoretic separability in heredity of the germinal "determiners" or "factors" of characters is in full accord with the several aspects of separability in evolution previously observed in paleontology, embryology and individual development.

The purpose of this synopsis is to review and bring together some of the noteworthy phenomena of character separability as contrasted with those of interdependence, cooperation, correlation and coordination.

It is probable that this principle of separability of units of function and structure, which has been discovered in so many processes of the organism, will prove to be a universal principle. This principle is more or less a necessary consequence of the unit-cellular structure of the organism; if instead of being composed of cell units, each possessing its peculiar heredity qualities, an organism were composed of fluid or solid masses of different kinds, we can not imagine how it could split up into character units. Yet the cell is probably not the ultimate, or least character unit, which is doubtless a chemicophysical unit. This is extremely suggestive in connection with our conceptions of the nature of the evolution process, for the process more or less clearly resolves itself into three problems, namely: (1) how do these character units arise; (2) how are these character units coordinated into harmonious action within the organism; (3) why do these character units independently evolve, progress or retrogress?

Since the word "character" is very vague, and since the term "unit character" has a special and limited meaning in Mendelian heredity, I propose the new term "biocharacter" as a general designation of the character unit in the organism.

1. KINDS OF BIOCHARACTERS OBSERVED IN PALEONTOLOGY

Biocharacters are those characters, large and small, which through the evidence afforded by ontogeny (*i. e.*, zoology, embryology), phylogeny (*i. e.*, paleontology), or heredity (Mendelian inheritance) are found to be separable from or independent of each other as units in the processes of heredity, of evolution, and of individual development.

Paleontology gives evidence no less positive than embryology and experimental heredity that each organism is made up of a number of such separable characters, including those known as the "unit characters" of Mendelian heredity. In paleontology this separability in heredity and evolution is found to apply to structural, or anatomical, characters of three principal kinds, namely, I, II, III:

I. *New orthogenetic characters (rectigradations of Osborn), characters having an adaptive evolutionary direction from the start, completely separable in heredity, so far as observed continuous in origin.*	II. *New numerical characters, presence and absence characters, meristic characters, characters either adaptive or non-adaptive, completely separable in heredity, so far as observed discontinuous in origin.*	III. *New proportional characters (allometrons of Osborn), quantitative and intensive characters. Generally separable, sometimes blending in heredity, so far as observed continuous in origin, adaptive or neutral.*
Examples	*Examples*	*Examples*
New horns, germinal separability. New dental cusps, germinal separability. Certain new dental folds and plications, germinal separability. Such rectigradations are relatively rare in titanotheres, and much more prevalent in the teeth of horses.	Such characters are of three kinds: (1) Abnormal, or teratological, *i. e.*, reduplication of parts already present, supernumerary digits, teeth, vertebræ, ribs, etc.; (2) normal, by added vertebræ, added ribs, added teeth, added phalanges; (3) minute saltations of structure, minor variations of Darwin. Evolution through the multiplication or diminution of existing parts.	Variations in size and proportions of existing units of structure, *i. e.*, evolution of skull and limb proportions, dolichocephaly, brachycephaly, platycephaly, dolichodactyly, brachydactyly; in brief, adaptive changes of proportion and intensity in existing characters and groups of characters.

The property of separability, divisibility, independence of these biocharacters stands in contrast to that of

their interdependence and coordination of function in the organism. As remarked above the discovery of this property of separability of characters was gradually prepared for in various branches of biology. First, in comparative anatomy, through the observations of the laws of independent degeneration, balance and progression of adjoining parts; second, through embryogeny and ontogeny, in the observation of the hastened or retarded development of adjoining parts; third, through heredity, as, for example, in the mosaic inheritance of Galton; fourth, through paleontology and phylogeny, in the law of acceleration and retardation of Hyatt and, through the observations of many other paleontologists, concluding with the detailed observations of Osborn and Gregory. But the property of separability first shone out clearly and most brilliantly in the discoveries of Mendel in heredity.

This property of structural separability and independence of evolution is closely connected with *separability or independence of function.* Thus separability may distinguish a great number of cells and tissues which are united by a single function, or separability may distinguish a single cell, as, for example, the single giant cells of the spinal cord of certain fishes and amphibians.

It is important, therefore, to realize that this property of separability, the separability of biocharacters, is now observable under six classes of evidence.

2. MODES OF SEPARABILITY OF BIOCHARACTERS IN HEREDITY, IN GENESIS, IN RATE OF EVOLUTION

I. *Biocharacter heritage separability,* unit or exclusive inheritance.

1. *Evidence of Galton, etc., as to mosaic inheritance.*
2. *Character heritage separability,* under the separate "determiner" or "factor" hypothesis of Mendel, Bateson, Morgan, etc., according to which each "biocharacter" of the soma may spring from one or more "determiners" or

"groups of determiners" in the germ. Many characters are not entirely separable, but tend to go in groups or to blend.

3. *Character heritage blending,* Castle, Osborn, etc., as observed in color, size, proportion, etc.

II. *Separability in genesis, biocharacter origin and evolution.*

1. *Origin through saltation,* large heritable leaps (*saltus,* a leap, syn. discontinuity, Bateson).
2. *Origin through minute heritable gradations* (*gradus,* a step), Darwin (minute heritable variations), De Vries (mutations).
3. *Origin through continuity* (*continuatio,* an unbroken series; continuous describes that which is absolutely without pause or break, in contrast to saltation = leaps, gradation = steps). It has been shown (Osborn) that characters continuous in origin may be separable or discontinuous in heredity, as in both the new rectigradations and new proportion characters of the hybrid of the horse and the ass.
4. *Continuous rectigradations,* Osborn, *i. e.,* orthogenetic or adaptive origin followed by adaptive evolution in a single direction, a principle probably corresponding with the *Mutationsrichtung* of Neumayr.
5. *Homomorphic* (Fürbringer) *rectigradations, through independent origins,* the independent production of similar biocharacters in organisms of similar ancestral affinity, the "potential homology" of Osborn, as distinguished from the true homogeny, homology *sensu strictu,* of direct descent of characters from each other.
6. *Mutations of Waagen,* subspecific steps or gradations in evolution of characters under the *mutationsrichtung,* or trend of development in certain directions, of subspecific value, *i. e.,* intergradations between species.

III. *Separability in velocity, biocharacter motion* (*i. e.*, rate of transformation, or relative displacement).

1. *Ontogenetic acceleration,* hastening of development in ontogeny, resulting in certain biocharacters appearing at earlier and earlier stages of development. Hyatt's law.
2. *Ontogenetic retardation,* slowing down of biocharacters in ontogeny, resulting in certain biocharacters appearing at later and later stages of development. Hyatt's law.

1 and 2 result in heterochrony (Gegenbaur).

3. *Ontogenetic balance,* resulting in biocharacters appearing at the same stage as in the ancestral forms.
4. *Phylogenetic acceleration,* appearance of certain homomorphic biocharacters at earlier geologic periods in some phyla than in others.
5. *Phylogenetic retardation,* whereby some homomorphic biocharacters appear at later geologic periods in some phyla than others.
6. *Phylogenetic balance.*

IV. *Separability in grouping, biocharacter cooperation and coordination.*

A biocharacter may be closely linked with others in group function or it may detach itself and connect with another group, *e. g.*, color and speed biocharacters in horses.

1. *Biocharacter correlation into similar adaptive character groups.*
2. *Biocharacter grouping through heredity,* attributable to prolonged ancestral grouping.
3. *Biocharacter compensation,* the gain of one character at the expense of another. The law of compensation of St. Hilaire.
4. *Biocharacter sex linkage,* the union of groups of characters with the function of sex as family or secondary sexual characters.

V. *Separability in proportion characters. Character proportion genesis, separability in the evolution and heritage of proportions.*

1. *Proportion genesis through fluctuation,* theoretically through continued selection of plus and minus variations in a given direction in cases where such variations of proportion are of adaptive significance, as in fluctuating variations of length of neck in the giraffe.
2. *Character proportion continuity in zoologic and paleontologic series,* the unbroken succession in the evolution of changes of proportion, as in brachycephaly and dolichocephaly in kindred races of man.
3. *Character proportion saltation, in hybrids only,* sudden appearance of profound changes of proportion, as in the Mouchamp breed of sheep.
4. *Character proportion heritage separability.* Complete separation in heredity of certain proportional characters, as in crosses between dolichocephalic and brachycephalic types in man.
5. *Character proportion heritage blending,* the origin of blended, or intermediate, forms of certain proportional characters in man and horses.
6. *Character proportion genesis,* partly at least through interaction of separably specific harmones, chalones, internal messengers of the thyroid and other internal secreting glands.

VI. *Separability in orthogenesis, rectigradations, genesis of new adaptive characters from infinitesimal beginnings.*

1. *Independent genesis of similar adaptive characters* in different phyla giving rise to homomorphy.

2. *Evidence of hereditary predetermination or potentiality* of the genesis of similar new characters in phyla derived from similar ancestors.
3. *Continuous evolution of rectigradations in one direction, Mutationsrichtung.*
4. *Mutations of Waagen,* subspecific gradations of character.
5. *Complete separability of rectigradations in heredity,* as shown in the teeth of the hybrids of the horse and ass, all rectigradations being either present or absent but not blended.

3. SUMMARY

It appears from the foregoing classes of evidence that biocharacters are separable in origin, development, evolution, and heredity. First, biocharacters are separable through their many different modes of origin from the germ, either saltatory, gradational, or continuous. Second, biocharacters have different rates of motion, or velocity, in individual development (ontogeny), exhibiting acceleration or retardation. Third, biocharacters have different rates of evolution in different phyla (phylogeny), again exhibiting acceleration or retardation (phyla). Fourth, all the biocharacters of an organism cooperate through various modes of grouping in functional correlation, in compensation, in sex linkage. Fifth, in the hard parts of the body while the biocharacters of form and proportion may originate through continuity, through saltation, or through minute gradations, all the known evolution of proportion biocharacters is continuous. Sixth, in the hard parts the biocharacters of rectigradations have only been observed to originate and develop through continuity.

EVIDENCE OF MULTIPLE FACTORS IN MICE AND RATS

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THE object of this paper is to record certain data on the inheritance of two complex characters and analyze these data together with those obtained in certain analogous experiments by other investigators. This is done with a view to ascertaining what they contribute to our knowledge of the relative merits of the two more or less contradictory hypotheses, multiple segregating factors or a single fluctuating factor which are being advocated by geneticists to explain certain cases of inheritance.

It will be useful at the outset to state in a somewhat definite manner how the alternative hypotheses differ from one another. MacDowell (1916) in a recent paper has clearly and precisely defined the two views. From this start the following statement may be made. The first view supposes that variations of the germ plasm are in the nature of fluctuations. The germ plasm is in a continuous state of variation. The hereditary characters all vary under observation and this is taken to mean that the factors in the germ plasm determining them also vary. Fluctuation in the character is measured and used as a means of detecting and recording a similar though not identical variation in the germinal factor underlying and determining the character under observation. To use a concrete example. In a given species the individuals are of various sizes, some larger, some smaller. Some of this variation is considered as in part due to non-heritable environmental influences. There is, however, a distinct "inheritance" of size. This is considered the result of a variable germinal factor which as Castle suggests may be "Perhaps some substance or ferment which varies in

amount, larger amounts producing larger results" (1916, p. 55). In crosses between animals possessing distinctly different degrees of the size "factor" blending rather than alternative inheritance is supposed to result. This also holds in the case of crosses between races differing only slightly in the degree of the size character. In such cases says Castle "we do not find it easy to detect segregation" (1916, p. 55).[1]

The "second" view supposes that complex physiological results such as the "size" of a certain animal depend upon a complex of genetic factors. All these factors are concerned in the growth and therefore the size of the animal. The germinal determiners of these many factors are considered to be units.[2] As such their behavior in inheritance is definite, non-blending, and essentially Mendelian in nature. The blending, fluctuating nature of the character studied is supposed to be due to environmental factors, to the large number of hereditary factors involved, and to absence or incompleteness of dominance.

With this rather incomplete statement we may turn to an examination of the experimental data.

I. The Inheritance of Spotting in Mice

Experiments on the inheritance of spotting in mice have been carried on by the writer since 1909. As they progressed it became evident that spotting in mice offered remarkable material for the investigation of the inheritance of a variable character. Spotting as a character is easily measurable and classifiable. It is not affected by changes in the external environment. Variations in

[1] It is interesting to note in this connection, the quotation from Castle given by MacDowell, 1916, page 741, describing the inheritance of minute quantitative differences in intensity of yellow pigmentation in guinea-pigs. The later work of Wright, 1915, also has a distinct bearing on this particular case in that it shows four truly allelomorphic grades of intensity of pigmentation in guinea-pigs. Fluctuation occurs about these four variation centers and Castle's "complete series of intermediates" between red and cream color in guinea-pigs is broken into three distinct centers of variation with overlapping range.

[2] East, 1912, has made clear the fact that variation within the unit, under certain conditions must of course be supposed to be possible.

degree of spotting are almost certain to be quickly recognized.

In mice a so-called recessive "piebald" spotting has long been known. In addition a distinctly different hereditary type, commonly dominant, was recorded by Miss Durham (1911), and was further investigated by the writer who found it to be entirely independent in inheritance from the "piebald" type. This "dominant" spotting I have called the "black-eyed white" type of spotting. Further in 1914 a third type of spotting known as "blaze," consisting primarily of a white forehead spot, was reported on by the writer. This type has since been found to be independent of the other two in inheritance. The existence of at least three genetically distinct types of spotting in mice is therefore proven. It is not the purpose of this paper to generalize from this fact, *but to attempt to show that various grades of a single type of spotting may be introduced into a cross and may reappear in the F_2 or back-cross generation, not rarely, but in a considerable proportion of the animals obtained.* This is a common breeding test of segregation as compared with contamination and of alternative as compared with blending inheritance.

The races of mice used offer for the most part extremely homogeneous material. The experimental animals come from closely inbred races which have undoubtedly reached a degree of genetic homogeneity which would lead to definite results in breeding, and a clearer opportunity to observe segregation if it existed. The degree of white spotting in the races of piebald mice used is estimated by recording the approximate per cent. of the dorsal surface which is pigmented. This method is subject, as is any system of arbitrary grades, to a certain amount of error. It is, however, reasonably accurate and affords a fair measure of the degree of pigmentation of any individual.

The first experiment to be recorded is a cross involving an English piebald race descended from black-eyed white mice (Little, 1915). These piebalds vary in the extent of dorsal pigmentation from 20 to 96 per cent. It

will be seen from Table I that there are essentially two modes to the variation curve, one of these occurring at 30 to 44 per cent., and the other at from 80 to 92 per cent. Animals from this race were crossed with dilute brown self mice, and with mice from a yellow and from a mixed black-agouti and black race. The F_1 generation consisted of solid colored young. When these F_1 self young were crossed back with animals from the piebald race, a range of variation was obtained which is shown in the second line of Table I.

TABLE I

PERCENTAGE OF DORSAL PIGMENTATION

	0–4	5–8	9–12	13–16	17–20	21–24	25–28	29–32	33–36	37–40	41–44	45–48	49–52	53–56	57–60	61–64	65–68	69–72	73–76	77–80	81–84	85–88	89–92	93–96
Piebald English stock..	—	—	—	—	2	2	11	27	18	26	18	9	14	6	10	4	12	2	7	17	13	16	15	1
Back-cross piebald....	—	—	—	—	—	—	1	1	6	13	6	7	10	2	11	2	6	1	3	5	6	10	10	5

It will be seen that even though the total of the young obtained is less than in the pure piebald race, its range of variability is essentially the same and there are only four animals among those raised from the pure piebald race which fall outside of the range of variation of the back-cross generation. There is, moreover, no evidence of a single mode in the curve of the back-cross generation, but the modal centers of the parent piebald race are each represented by a large number of young in the back-cross generation.

Another cross in which larger numbers have been recorded is one between Japanese spotted mice and two races of self pigmented mice raised at the Bussey Institution. About two years before the self mice were crossed with the Japanese, certain spotted mice of common ancestry with them were separated off as a different stock. The range of variation in the degree of spotting within this last named race may be considered a fair indication of the probable appearance of the self animals used if they had been spotted. It will be seen from

the first row of Table II that, in this race, animals varying from 56 to 96 per cent. were obtained. There is a tendency for a mode to be formed between 80 and 92 per cent. The Japanese race used is one which for several years has been closely inbred and which holds remarkably true to type. Its range of variation is shown in the second row of Table II. It will be seen that the animals possess from 4 to 36 per cent. of the dorsal surface pigmented. A distinct mode is observed between 13 and 16 per cent.

TABLE II

PERCENTAGE OF DORSAL PIGMENTATION

	0–4	5–8	9–12	13–16	17–20	21–24	25–28	29–32	33–36	37–40	41–44	45–48	49–52	53–56	57–60	61–64	65–68	69–72	73–76	77–80	81–84	85–88	89–92	93–96
Tame race...	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	1	6	10	5	13	11	10	19	9
Japanese spotted....	1	8	74	92	65	23	7	4	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F_2 spotted...	—	—	—	—	3	2	5	6	4	10	6	5	9	3	11	5	6	4	8	10	8	9	14	18
Back-cross spotted Gen. 1....	—	—	3	2	4	4	14	14	14	16	5	13	8	7	4	1	6	3	—	2	1	2	5	8
Back-cross spotted Gen. 2....	—	1	1	1	—	—	1	1	—	5	4	6	5	1	3	1	—	1	—	1	—	—	3	3

The F_1 generation obtained from crossing the Japanese race with the self dilute brown or brown agouti animals above referred to, consists of solid colored animals and is therefore not to be recorded. The F_2 generation in which 146 piebald animals have been recorded contains mice ranging from 20 to 96 per cent. pigmented. Among the 146 animals recorded, 20 or 13.6 per cent. fall in grades characteristic of the Japanese grandparents. 94 or 63.6 per cent. are of grades found in spotted animals of the other grandparental race, see Table II, line 3. Two other generations of great interest have been tabulated. The first of these, line 4, Table II, is the result of back crossing F_1 generation animals with animals of the Japanese parent race. In this generation there is distinct evidence of segregation. Fifty-five of the 131 animals recorded fall within the limits of the Japanese grand-

parental race and 35 within the variation limits of the other grandparental spotted ancestor, and of these an appreciable number occur at the upper limit of variability, there being no evidence of a tapering of the curve at this point. This fact would appear to be of marked significance. When first generation back-cross animals are bred *inter se*, a second back-cross generation is produced, which, though it includes only 38 animals, has given extremely interesting results, see line 5, Table II. There are five animals which are distinctly Japanese segregates, and of these three show a degree of pigmentation which would make them easily mistaken for even the extreme variants in the Japanese race. At the other end of the curve it is interesting to note that six of the thirteen young reproducing the condition of the non-Japanese grandparental stock, fall into the two extreme upper classes and may be considered as true segregates rather than due to any chance occurrence of an abnormal physiological condition.

A third cross involving spotted mice has been made. This is between animals showing a small white forehead

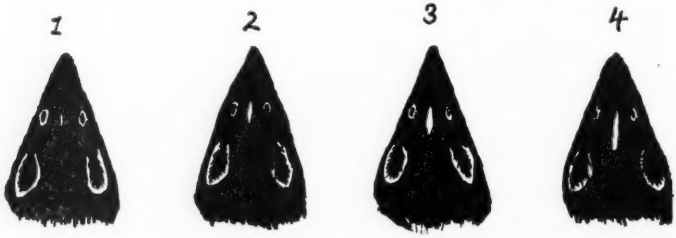

FIG. 1

spot and a self race. The dilute brown self race used for one parent is the same that has been already recorded above in the second experiment with mice. The range of variation of white spotting in the blaze or forehead spot race used, is recorded in line 1 of Table III. The grades of spotting designated in Fig. 1, numbers 1 to 4, represent the increasing degrees of white spotting. The animals comprising this spotted race are all of them pure

wild mice descended from a few individuals captured at Forest Hills, and at Wenham, Mass. The F_1 generation obtained by crossing the "blaze" and dilute brown self races is all self in character. The F_2 generation shows a distribution of young recorded in line 2, Table III.

TABLE III

GRADE OF SPOTTING

	−½	1	1½	2	2½	3	3½	4
Pure blaze animals	7	21	4	20	6	5	3	2
F_2 blaze animals	3	15	1	16	10	7	3	1
F_3, F_4, F_5 blaze animals	25	136	24	107	25	55	7	11

It will be seen that the extremes of variability in F_2 are the same as in the pure inbred wild blaze race. F_3, F_4, and F_5 animals raised *without selection* give a result recorded in line 3 of Table II, and again show the same limits of variation. It will be seen, therefore, that the blaze character is segregated from the cross without apparent modification, although the extremely minute degrees of spotting which it includes are those which one might expect would be modified or entirely swamped if contamination between the gametes of the self and blaze races occurred. This cross together with the cross between mutant and wild rats recorded by Castle to be considered later, give conclusive evidence that even a minute quantitative character segregates after crossing and does not afford grounds for the objection raised by Castle that crosses between races differing slightly in size or like fluctuating characters do not readily show segregation.

To sum up the results of spotting inheritance in mice, it may be said that all the crosses made show a reappearance of grandparental conditions in F_2, back-cross, and other advanced hybrid generations. The reappearance of these grandparental types is frequent enough to lead one to conclude that if segregation in a strictly Mendelian sense is not taking place, that at least the outward appearances of such a process are all of them present.

II. THE INHERITANCE OF SPOTTING IN RATS

Castle's work on the inheritance of fluctuations in the hooded coat pattern of rats is well known to all geneticists, and may now be considered in an attempt to examine the bearing of spotting on the inheritance of fluctuating characters in general. The hooded rats with which

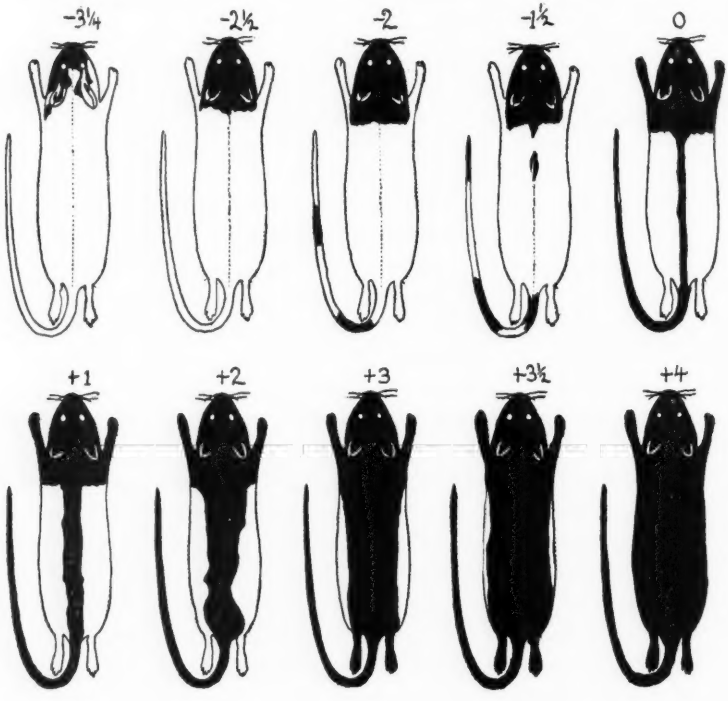

FIG. 2

In grades higher than +4 the whole dorsal surface is pigmented and the ventral surface is becoming progressively more so.

Castle worked have been shown clearly by Doncaster, Mudge, and others, as well as by Castle himself, to be recessive to self or solid colored coat in inheritance. The hooded pattern is, however, subject to wide fluctuation producing a series of rats from those with the whole dorsal surface and most of the ventral surface pigmented,

to rats in which only small spots around the eyes remain pigmented. The following diagram will show roughly the limits of variation and some of the intermediate types as graded by Castle. Throughout the course of his selection experiments, Castle has at times crossed the plus variants with the minus variants or else crossed selected animals from the plus or minus series with wild or with Irish rats. Both the last mentioned varieties are essentially self pigmented animals and are dominant in inheritance to the hooded pattern. The race with which Castle started his selection experiments showed within the first two generations of selection rats varying from grade minus two to grade plus three and three quarters.

Castle and Phillips, 1914, have recorded the results of two crosses between minus variants and plus variants. The first of these crosses was between females of minus two grade in the sixth selection generation and males of plus three and one half or three and three quarters grades in the fifth selection generation. It is possible to use the range of variation among the progeny of animals of these grades within the selection generation from which they are chosen to control the results of the cross. In Table IV[3] the first line represents the range of variation in the progeny of minus two animals of the sixth selection generation. The second line represents the range of variation in the progeny of plus three and one half and three and three quarters animals of the fifth selection generation. It will be seen that there is a space of seven grades between the two limits of variation of the parent races. The cross between these two types produced in the F_1 generation a range of variation shown in the third line of Table IV. It will be seen that for the most part, the young fall in the seven classes between the two parent races. In these seven classes will be found sixty-eight or 73.1 per cent. of the ninety-three young. Two or 2.27 per cent. of the young show grades of pig-

[3] The references to tables and pages appearing in the first column of Table IV, and ensuing tables, refer to Castle and Phillips, 1914.

TABLE IV

Generation	−3	$2\frac{3}{4}$	$2\frac{1}{2}$	$2\frac{1}{4}$	2	$1\frac{3}{4}$	$1\frac{1}{2}$	$1\frac{1}{4}$	1	$\frac{3}{4}$	$\frac{1}{2}$	$-\frac{1}{4}$	0	$+\frac{1}{4}$	$\frac{1}{2}$	$\frac{3}{4}$	1	$1\frac{1}{4}$	$1\frac{1}{2}$	$1\frac{3}{4}$	2	$2\frac{1}{4}$	$2\frac{1}{2}$	$2\frac{3}{4}$	3	$3\frac{1}{4}$	$3\frac{1}{2}$	$3\frac{3}{4}$	4
−2 rats, Table 22, p. 41	—	—	3	22	324	368	119	60	51	14	8	—	—	—	—	—	—	—	—	1	2	11	5	18	33	67	54	63	30	6
$+3\frac{1}{2}$, $+3\frac{3}{4}$ rats, Table 6, p. 34	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—
F_1, Table 50, p. 51	—	—	—	—	—	2	—	2	1	8	10	13	25	2	8	11	6	3	1	—	—	—	—	—	—	—	—	—	—	—
F_2, Table 50, p. 51	—	—	—	—	1	4	9	7	22	24	26	20	49	10	24	24	23	10	20	13	7	5	7	—	—	—	—	—	—	—

TABLE V

Generation	$3\frac{1}{2}$	$3\frac{1}{4}$	−3	$2\frac{3}{4}$	$2\frac{1}{2}$	$2\frac{1}{4}$	2	$1\frac{3}{4}$	$1\frac{1}{2}$	$1\frac{1}{4}$	1	$\frac{3}{4}$	$\frac{1}{2}$	$-\frac{1}{4}$	0	$+\frac{1}{4}$	$\frac{1}{2}$	$\frac{3}{4}$	1	$1\frac{1}{4}$	$1\frac{1}{2}$	$1\frac{3}{4}$	2	$2\frac{1}{4}$	$2\frac{1}{2}$	$2\frac{3}{4}$	3	$3\frac{1}{4}$	$3\frac{1}{2}$	$3\frac{3}{4}$	4	$4\frac{1}{4}$	$4\frac{1}{2}$
$-2\frac{3}{4}$, $-2\frac{7}{8}$ rats, Table 26, p. 41	1	2	1	1	3	5	11	6	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
$+3\frac{3}{4}$ rats, Tables 10 and 11, p. 36	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	9	13	65	124	46	8	1	—
F_1, Table 50, p. 51	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	1	2	4	2	1	1	—	1	—	—	—	—	—	—	—	—	—	—
F_2, Table 50, p. 51	—	—	—	—	—	—	—	—	—	2	—	4	3	8	8	12	9	6	5	3	5	2	2	1	2	1	—	—	—	—	—	—	—

mentation characteristic of the plus parent and twenty-three or 24.75 per cent. of the young show grades characteristic of the minus parent race. When the F_1 young are bred *inter se* there is a marked increase in the per cent. of young showing grades of pigmentation characteristic of the grandparents. Ninety-three, or 30.5 per cent., of the 305 F_2 generation young fall in grades characteristic of the minus grandparents. Fifty-two, or 17.0 per cent., fall in grades characteristic of the plus grandparents. The remainder, or 52.5 per cent., fall in the seven intermediate classes.

A second cross made between selected animals is shown in Table V. Females of grade plus three and three quarters of the tenth selection generation were crossed with a male of grade minus three and one quarter of the tenth selection generation. As a control for the females it is possible to use the progeny of grade three and three quarter parents in the tenth and eleventh generations. The reason for using two generations instead of one is in order to increase the number of progeny available, since the tenth generation alone shows such a small number of young that they are not valuable as a significant breeding test. The range of variation in the progeny of rats of this grade is shown in the second line of Table V. As controls for the minus parent, rats of grade minus two and three quarters and two and seven eighths of the tenth selection generation have been used. Although the total of the young produced by them is very small (thirty-one), it is, nevertheless, the only critical data available. The range of variation of these young is shown in the first line of the table. The F_1 generation resulting from the cross of these two diverse selection types is shown in the third line of Table V. The thirteen young comprising this generation all fall in grades between the two parent types. The F_2 generation shows a distinctly greater variability than the F_1 generation and includes four young of grades characteristic of the plus grandparental race. This cross is less conclusive than the previous cross, but

TABLE VI

Generation	3¼	3	2¾	2½	2¼	2	1¾	1½	1¼	1	¾	½	−¼	0	+¼	½	¾	1	1¼	1½	1¾	2	2¼	2½	2¾	3	3¼	3½	3¾	4	4¼	4½	4¾
−1¾ Parents, Tables 17 and 18, p. 39	—	—	—	—	—	9	8	12	13	33	10	3	2	—	—	—	—															
F_2, Table 42, p. 48	—	—	—	—	—	—	—	2	—	4	6	5	6	13	2	1	3	4	5	3	4	2	1	—	—	—	1	—	—	—	—	—
−2 Parents, Table 22, p. 41	—	—	—	3	22	324	368	119	60	51	14	8	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	—	—	—
F_2, Table 42, p. 48	—	—	—	—	—	—	1	1	1	1	2	6	6	7	2	3	6	4	2	4	1	—	—	—	1	—	—	—	—	—	—	—
−2⅛ Parents, Table 25, p. 42	1	—	4	22	78	251	100	15	1	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F_2, Table 42, p. 48	—	—	—	—	—	1	3	3	1	10	3	9	8	14	—	4	7	8	1	4	3	5	2	4	1	—	—	—	—	—	—	—
+3 Parents, Table 4, p. 33	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	7	12	25	19	35	29	9	4	1	—	—	—	—
F_2, Table 42, p. 48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	5	3	2	3	4	2	1	—	—	—	—	—
+3¼ Parents, Table 6, p. 34; +3½ Parents, Table 7, p. 35	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	9	12	17	47	62	59	59	49	4	1	—	—
F_2, Table 42, p. 48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	2	1	1	1	6	9	8	8	1	—	—	—	—
+4¼ Parents, Table 11, p. 36	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	2	13	5	3	1	1
F_2, Table 42, p. 48	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	3	4	2	3	3	—	—	—	—

TABLE VII

Generation	−2¾	2½	2¼	2	1¾	1½	1¼	1	¾	½	¼	0	+¼	½	¾	1	1¼	1½	1¾	2	2¼	2½	2¾	3	3¼	3½	3¾
−1½× Parents, Table 20, p. 40; Table 19, p. 39	—	1	—	13	23	15	17	16	16	5	3	2	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F_2, Table 43, p. 48	—	—	—	1	5	3	6	12	26	9	9	10	1	3	2	2	1	—	—	—	—	—	—	—	—	—	—
−1⅞ Parents, Table 20, p. 40	—	—	6	31	50	29	12	11	4	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F_2, Table 43, p. 48	—	—	—	—	6	3	4	5	9	14	8	1	—	1	1	1	—	—	—	—	—	—	—	—	—	—	—
−2 Parents, Tables 23 and 24, p. 41	7	19	76	843	818	158	26	51	9	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
F_2, Table 43, p. 48	—	—	—	6	6	12	11	8	3	4	4	6	1	3	—	—	—	—	1	1	—	—	—	—	—	—	—
+2¼ Parents, Table 2, p. 32	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	1	3	1	1	—	1	—	—	—	—
F_2, Table 43, p. 48	—	—	—	—	—	—	—	2	4	5	4	16	7	16	22	25	29	24	13	33	14	8	8	6	3	—	—
+3 Parents, Table 4, p. 33	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	1	7	12	25	19	35	29	9	4	1
F_2, Table 43, p. 48	—	—	—	—	—	—	—	2	—	—	—	1	1	3	3	4	2	2	1	2	1	1	—	—	—	—	—

does nevertheless show that 5.4 per cent. of the seventy-three F_2 young reproduce the degree of spotting characterizing one of the parental races.

The total number of animals observed, however, is considerably smaller than in the previous experiment and the results are therefore subject to greater error.

We may now consider several crosses made between hooded and wild rats. The F_1 generation in such crosses consists almost entirely of self pigmented animals. It is, therefore, in a comparison of the range of variability observed in the F_2 generation with that observed in the pure hooded race from which the hooded grandparent was taken, that we may expect to find evidence for or against segregation. The first cross to be recorded is between a female of grade $-1\frac{7}{8}$ in the $2\frac{1}{2}$ generation of the minus selection series, and a wild male. As a control for this female, the progeny of $-1\frac{3}{4}$ parents in the second and third selection generations may be taken. It will be seen that their progeny varies between grades -2 and $-\frac{1}{4}$ (see line 1, Table VI), in a total of 90 animals. The F_2 generation shows a range of variability between grades $-1\frac{1}{2}$ and grade $+3\frac{1}{2}$. It is interesting to note, however, that twenty-three or 37 per cent. of the sixty-two animals observed fall within the range of variation of the hooded grandparent. A comparison of grades $-1\frac{1}{2}$ and -2 in Fig. 2 will show how closely F_2 animals approach the extreme condition of the hooded grandparental race.

In the second cross between hooded and wild rats, females of minus two grade of the sixth generation of the minus selection series were used. As controls for these females the progeny of -2 parents in the sixth generation of the minus selection experiment may be used (see line 3, Table VI). The 969 young so obtained fall between the grades $-2\frac{1}{2}$ and $-\frac{1}{2}$. The forty-eight young show a large range of variability from $-1\frac{3}{4}$ to $+2\frac{3}{4}$. Of the forty-eight obtained, twelve, or 25 per cent., fall within the range of variation of the progeny of the hooded grandparental generation.

The third cross was between wild males and females of grade -2 or $2\frac{1}{4}$ in the tenth generation of the minus selection series. As a control for these animals it is possible to use the progeny of $2\frac{1}{8}$ parents in the tenth generation of the minus selection series (see line 5, Table VI). The 474 young so obtained vary between grades $-3\frac{1}{4}$ and -1.

Among the ninety-one F_2 young obtained, eighteen, or approximately 20 per cent., fall within the limits of variability of the hooded grandparents. The range of variability in the F_2 generation is considerable, being from -2 on one side to $+2\frac{3}{4}$ on the other.

Three crosses between animals of the plus selection series and wild rats are recorded. In the first cross (see lines 7 and 8, Table VI) females of grade plus three of the third generation of the plus selection series were used. The breeding capacity of these animals may be fairly judged by considering the progeny obtained from plus three parents in the third generation of the plus selection experiment. The 143 young so obtained range from grade $+\frac{3}{4}$ to $+3\frac{3}{4}$. Only twenty-one F_2 young are recorded, varying between grades $+1\frac{3}{4}$ and $+3\frac{1}{2}$. It is interesting to note that *all of them fall within the range of variation of the grandparental hooded race.*

In the second cross females of grade $+3\frac{1}{4}$, fifth generation and females of grade $+3\frac{1}{2}$, sixth generation, were crossed with wild males. The progeny obtained from animals of similar grade and generation within the selection experiment can serve as controls. The 320 young so obtained vary between grades $+1\frac{1}{2}$ and $+4\frac{1}{4}$. The thirty-eight F_2 young obtained vary between grades $+1\frac{1}{2}$ and $+3\frac{3}{4}$, again, in every case, reduplicating the grandparental forms.

The third cross, which includes only small numbers and is therefore of less relative value than the two previous crosses, was between a female of $+4\frac{1}{4}$, tenth generation and a wild male. The control animals gave twenty-five young ranging from grades $+3\frac{1}{2}$ to $+4\frac{3}{4}$. The F_2 gen-

eration, which consists of only sixteen animals, ranges between the grades $+2$ and $+3\frac{3}{4}$. Six of the sixteen young fall within grades characteristic of the grandparental animals (lines 11 and 12, Table VI).

Crosses between hooded and Irish rats have given comparable results (Table VII). Rats of grades $-1\frac{1}{2}$ generation $3\frac{1}{2}$ minus selection, were crossed with Irish rats. As a control for the hooded animals the progeny of rats of grade $-1\frac{1}{2}$ in the third and fourth selection generation may be used. The total of the progeny so obtained is 112. It will be noticed from Table VII, line 1, that they vary between grades $-2\frac{1}{2}$ and $+\frac{1}{4}$. Only eight or 8.8 per cent. of the F_2 generation vary *outside* of the grandparental grades. The range of variability in this generation is between -2 and $+1\frac{1}{4}$. The second cross is between females of grade $-1\frac{7}{8}$, from the fifth selection generation of the minus series and Irish males (lines 3 and 4, Table VII). As a control for these the progeny of $-1\frac{7}{8}$ parents of a similar generation may be used. The 143 progeny so obtained fall within the grades $-2\frac{1}{4}$ and $-\frac{3}{4}$ inclusive. The fifty-three F_2 young range between grades $-1\frac{3}{4}$ and $+1$. Almost exactly 50 per cent. of them reproduced the grades of the hooded grandparental types.

The third cross is between females of minus two grade in generation $7\frac{1}{2}$ of the minus selection experiment and Irish males. As a control, the progeny obtained from the females of -2 grade in the seventh and eighth selection generations may be used. Such animals produced 2,013 young, ranging from $-2\frac{3}{4}$ to $-\frac{1}{2}$. Sixty-six F_2 young ranged from grades -2 to $+2$. Of these, 75.8 per cent. reproduced the grades characteristic of the hooded grandparental race.

Two experiments are recorded showing crosses of plus selection animals with Irish males. In the first of these, the females used were of grade $+2\frac{1}{4}$ in the second generation of the plus selection experiment. Animals of similar grade and generation may act as controls, although the number of young obtained from them is very small.

The eight young so obtained fall between grades $+1\frac{1}{4}$ and $+2\frac{3}{4}$. From this cross 239 F_2 young have been obtained ranging from grades -1 to $+3\frac{1}{4}$. 129 or 53.9 per cent. show grades characteristic of the hooded grandparent.

The remaining cross was between females of grade $+3$, third selection generation and Irish males. Controls obtained by tabulating the progeny of animals of similar grade and generation show in 143 young, a range between grades $+\frac{3}{4}$ and $+3\frac{3}{4}$. Only twenty-three F_2 young were obtained, ranging between -1 and $+2\frac{1}{4}$. Of these, sixteen, or 69.5 per cent., reproduce the grades characterizing the hooded grandparent.

One other striking cross is recorded by Castle in the case of the rats. This is a cross between "mutant" rats showing a particularly advanced degree of plus pigmentation and pure wild rats. The range of variability of the pure "mutant" race is according to Castle's statement (Castle and Wright, 1916, page 173) between grades $+5\frac{1}{4}$ and $+5\frac{3}{4}$, see Table VIII. The 109 F_2 "mutant" young show a range of variation between the same grades. According to Castle's statement on page 174, "their range of variation does not fall beyond that of the uncrossed mutant race." It would appear as though the evidence of segregation in this case, even to an almost exact degree, was clear. This case, together with that of the type of spotting in mice known as "blaze" (Little, 1914) already discussed, appears to show that races differing from each other in only a minute degree of a quantitative character may show segregation clearly.

TABLE VIII

Generation	+5	$5\frac{1}{4}$	$5\frac{1}{2}$	$5\frac{3}{4}$	$5\frac{3}{4}$
Pure mutants	2	4	28	17	—
F_2 mutant × wild	1	6	49	50	3

To sum up the experiments with rats, it may be said that while it can not be claimed that the evidence is final in regard to the unit nature of the factors involved, they

offer distinct evidence of segregation. That is to say, the combination of gametes formed by hybrid parents reproduce the same zygotic types as did combination of gametes of the pure parent races.

The bearing of the results on the practical breeding of farm animals seems clear. If a complicated and highly variable character as the hooded pattern in rats may be introduced in a cross with a non-hooded form and may be recovered in a large proportion of the F_2 generation, we may encourage crossing as a favorable method of producing new and important breeds. This will be all the more apparent if we agree with the selectionists who hold that the character reappearing in F_2 will be at once amenable to selection and improvement in a desired direction. *Contamination of genes* in breeding experiments which are conducted on a large scale and are followed by rigid selection, need not be considered as a factor of prime importance.

III. Physiological Factors Underlying Growth of Implanted Tissue

The study of the inheritance of spotting in mice and rats has served to give a considerable amount of data more or less directly comparable to that obtained in studies of size inheritance; though presenting, as I shall try to show, certain advantages in their freedom from environmental and age influences and in their definiteness.

We may now consider a very different line of work, which bears a most interesting relation to other studies of the inheritance of complicated morphological and physiological characters. The reaction of various closely inbred strains of mice and their hybrids to implants of a single tumor is definite, and characteristic. It is moreover undoubtedly hereditary as the work of many investigators has shown.

Tyzzer and the writer (1916) have reported results obtained in inoculating Japanese waltzing mice, closely inbred races of common mice and their hybrids, with an

epithelial tumor which originated in the Japanese waltzing race. The parent animals all of them came from races which, because of long continued inbreeding, may be considered to have reached a degree of great genetic homogeneity. It will be seen from the table (loc. cit., p. 403) that all the Japanese waltzing mice inoculated, 58 in number, grew the implanted tumor, while none of the common mice showed continuous growth of the tumor. This absolute difference between the parent races is extremely interesting and offers ideal material for the formation of intermediate conditions of susceptibility in hybrid generations. They further offer a test of the relative value of the hypotheses of multiple factor and of blending inheritance. Sixty-two F_1 hybrids obtained by crossing the Japanese with tame races were inoculated. Of these, sixty-one grew tumors. The tumors grew in most cases fully as rapidly if not more rapidly than in the susceptible Japanese parent races. It is probable that the one animal in this generation which failed to grow the tumor is not a true exception, but that its behavior may be due to poor technique. The second generation hybrids have given an extremely interesting result. Of the 183 inoculated, only three have shown continuous growth of the tumor. This result is surprising in view of the fact that susceptibility appeared to be a dominant character in the F_1 generation. Only thirty-eight animals of the F_3 generation were inoculated; none of them grew the tumor. The striking difference between the F_1 and the F_2 generations suggests at once, alternative rather than blending inheritance. As we have suggested in our previous paper, the most logical interpretation appears to be that a certain physiological condition on which the growth of the tumor depends, is produced in the animals of the Japanese waltzing race. This condition is not found in the tame mice used. The differences between the races are hereditary, since succeeding generations of the Japanese and tame mice behave like their parents. The fact that susceptibility of the tumor occurs in both F_1 and

F_2 generation hybrids shows that the conditions on which the growth of the tumor depends are reproduced in hybrids of the two races. The behavior of the F_1 hybrid generation produced by reciprocal crosses indicates clearly that even when only one of the parents is susceptible and comes from the homogeneous Japanese race, its contribution to its offspring is sufficiently powerful to produce susceptibility in that animal. In other words, we may say that the hereditary factor or factors underlying susceptibility are functional even when present in a "single dose." If there is a single general factor underlying susceptibility we should expect that the F_2 generation would show a large number of susceptible animals. This is not the case. It is possible, however, to consider the behavior of the F_1 generation as being largely due to heterozygosis and not to true inheritance. To eliminate this possibility a back-cross generation was made between F_1 animals and pure Japanese. The sixty-three animals comprising this generation all proved susceptible to the tumor and in a majority of cases grew it as rapidly as did the F_1 hybrids themselves. On the other hand, the F_1 generation crossed with tame mice gave seventy-eight young, all of which were non-susceptible.

In discussing the results, it was further suggested that the explanation which best fitted the facts, indeed the only explanation which fits all of the facts, is that susceptibility depends for its manifestation upon the simultaneous presence of several factors in either the homozygous or the heterozygous condition. The gametes of the Japanese race possess all or nearly all of these in a homozygous condition and therefore produce susceptible animals. The F_1 hybrids possess all of these factors in a "single dose"; they having been contributed by the Japanese parent, and are therefore susceptible. *When, however, the F_1 animals form gametes, these factors, if they are mendelizing and not blending in nature, will be distributed at random in the gametes.* The result will be that the larger the number of factors involved, the rarer will be the inclusion of

all of them within a single gamete formed by the F_1 animals. Since susceptibility in the F_2 generation will depend upon the presence of all of the factors ordinarily found in the Japanese race, it follows that the greater the number of factors involved, the rarer will be the appearance of a susceptible animal in the F_2 generation. It further follows that the susceptible animals of the F_2 generation probably will not possess the factors in a homozygous condition, as did the Japanese grandparents, and therefore they will not, in most cases, breed true, as did the Japanese grandparents, to the character of susceptibility.

For a more detailed discussion of these results from a genetic point of view, the reader is referred to Tyzzer and the writer's earlier paper. It will suffice at the present time to emphasize the fact that it is the inherent nature of the tissue of the host animal that is being studied. The tumor itself is as near a biologic constant as one can obtain. Variation in its growth therefore means variation in the attitude towards it, taken by the host tissue. This attitude appears to be dependent upon a complex of distinct factors. If a change or substitution is made in any one of the members of this complex, a different reaction is obtained. The behavior of the different factors in any such complex is distinctly that of independent units in inheritance. The fact that the reactions of susceptibility and non-susceptibility are dependent on multiple factors seems established. If the tissue of the adult mouse may be analyzed in this way, the conclusion is far reaching. If the reaction of the tissue depends on its substance, and its substance depends in turn on a certain hereditary complex of factors, it is logical to suppose that the rate and extent of development of the tissue as well as other processes of significance to the organism depend, in so far as they are hereditary, on similar complexes of genetic factors. Environment undoubtedly influences certain characters in their development far more than others, and in this respect size appears to be one of the most susceptible.

On the other hand, rate and extent of growth is undoubtedly chiefly dependent on the nature of the tissue involved, and as we have seen there is every reason to believe that this depends on the interactions of a complex of genetic factors which are independent of each other in inheritance.

Other Experiments with Inoculated Tumors in Mice

Loeb and Fleisher (1912) have reported a series of investigations on the hereditary factors underlying the susceptibility of mice to a transplantable carcinoma. As parent stocks they used three races of mice, one American race, and two European. By breeding tests including several generations the percentage of American mice to show continued growth of the inoculated tumor was found to be eighty-four, while those of the European races I and II were twenty-three and three per cent., respectively. The F_1 generation between American and European I gave sixty-eight per cent. susceptible, F_2 from this same cross gave thirty per cent. susceptible. When American mice were crossed with European II an F_1 generation was obtained in which one hundred per cent. of the animals inoculated were susceptible. Only fourteen animals were tested and the number is too small to establish this as an accurate percentage for this generation. The F_2 generation of this cross gave twenty-six per cent. susceptible.

It is interesting to note that in the F_1 generation, where sufficient numbers were obtained to afford critical evidence, the percentage of susceptibility was intermediate between those of the parent races. There is a marked decrease in degree of susceptibility in the F_2 generation. The fact that some of the animals of the American parent race failed to grow the tumors shows that this race is in all probability not homogeneous, and the same is true of the European races since animals within a single race fail to react similarly to pieces of biologically similar tumor. If such is the case, we should expect an intermediate result in the F_1 generation, just as we do when we cross two races differing in size. The F_2 generation should also be

intermediate, though *on the basis of blending inheritance we should expect the percentage of positive animals to be much closer to that observed in the F_1 generation than it actually is.*

On an hypothesis of multiple factors underlying susceptibility or immunity to the inoculated tumor the experimental results may well be explained. The F_3 generations of Loeb and Fleisher's work give a result further indicating the possible presence of multiple factors. If a large number of F_2 animals mated *inter se* at random are used to produce the F_3 generation the percentage of susceptible animals in F_2 should be roughly approached in the F_3 generation. 122 animals comprising the F_3 generation show twenty-four per cent. susceptibility as compared with thirty per cent. in the F_2 generation of the same cross. In the F_3 generation of the American times European II cross, sixty-six animals have been inoculated and have given only two per cent. of susceptibility. This difference is possibly due to the fact that F_2 animals forming gametes each closely resembling those of the grandparent European race were unconsciously chosen as parents for this generation.

The interesting part of Loeb's work is the fact that the relative homogeneity of the races of mice which he used approximate closely the conditions in respect to suceptibility and non-susceptibility which one ordinarily is dealing with in size crosses as, for example, Castle's work and also MacDowell's work with rabbits. In none of these cases has there been excessively close inbreeding in either parent race before crosses were made. There is, therefore, no definite complex of factors characterizing the race. As a result the percentage of susceptible animals varies and depends on the character of the particular animals used for breeding. The whole effect produced is to obscure the true nature of the processes involved. In respect to homogeneity the material at the disposal of Tyzzer and the writer possessed a great advantage which became apparent in the definite results produced.

Size inheritance studies have not been recently made with mammals of known ancestry and of approximately pure races. This fact greatly diminishes the value of the results obtained even though they represent work of the most painstaking sort. For this reason the writer started last January a series of experiments on size inheritance in pure races of rabbits. Polish rabbits are being used for the small parent and Flemish giant rabbits for the large parent. It is hoped by a careful study of variation within the pure races to understand more clearly the method of inheritance in the hybrid generations to be produced by later experiments.

To summarize the work with inoculable tumors, one may say that it presents a type of inheritance not explicable on an hypothesis of blending inheritance or of a single variable gene. All the results may, on the other hand, be satisfactorily explained by supposing that the nature of the host tissue and its reaction to the implant depend upon a complex of mendelizing factors.

Conclusion

The fact that three genetically distinct types of spotting exist in mice; that segregation of the degree of spotting occurs in both rats and mice; that segregation of minute quantitative characters like the "blaze" spotting in mice, and the pattern of the "mutant" rats occurs; and finally that the composition and reaction of epithelial tissue in mice depends upon a complex of mendelizing factors, all indicate that in mammals the multiple factor hypothesis is steadily being strengthened as a scientific theory and a practical principle of great interest and importance.

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THE INHERITANCE OF THE WEAK AWN IN CERTAIN AVENA CROSSES[1]

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(In cooperation with the Office of Cereal Investigations, U. S. Department of Agriculture.)

For some time past, the writers have had under observation many different hybrid series of oats. Certain of these offer an excellent opportunity for a study of the inheritance of awns. This paper is a preliminary report aiming to set forth ideas regarding the factor differences between certain types of awns, as a basis for a further study of the relation between awning and other characters of the oat grain.

Kinds of Awns

Practically all of the wild types of oats are characterized by a very strong awn. This awn is typically long, stiff, and geniculate. The basal portion of the strong awn is twisted in a clockwise fashion and either black or dark brown in color. Above the twist, the awn is practically straight until it reaches the knee, at which point it turns sharply and proceeds almost at right angles to its former course and usually in a different plane. The first step in the modification of this type of awn seems to be the loss of geniculation, together with a reduction of the stiffness. Then a further straightening of the awn occurs, leaving it practically straight from the point of attachment to the tip. Such a change is accompanied by a loss of the dark color at the base of the awn. An awn of this last type is usually spoken of as the *weak awn*. The weak awn may vary greatly in length, thickness, and rigidity. In some cases it becomes a mere hair-like appendage,

[1] Paper No. 62, Department of Plant Breeding, Cornell University, Ithaca, N. Y.

FIG. 1. Showing gradations between the spikelet possessing two strong awns, and the awnless spikelet. From left to right are shown: 2 strong awns; 1 strong and 1 weak awn; 1 strong awn; 2 weak awns; 1 weak awn; and the awnless type.

extending scarcely beyond the tip of the lemma and only distinguishable by careful examination. As this awn becomes weaker, it is produced nearer to the tip of the kernel; that is, the rib of the lemma which forms the awn adheres to the lemma for a greater distance before arising as an awn. Among the wild and cultivated types of oats the awns are either characteristically strong, weak, or lacking altogether. In hybrids of these, however, the awns may present all gradations between the awnless and the very strongly awned types. It is usually possible, though, to classify the hybrids as having strong, intermediate, or weak awns. (See Figures I and II.)

METHODS OF STUDY

The parent plants and first-generation hybrids were grown in the greenhouse, and the second and third generation hybrids were grown in the field. In the case of the first-generation hybrids, all of the spikelets on all of the plants could be studied. With the much larger F_2, however, it was found impracticable to attempt to study all of the spikelets on a plant. The study was limited,

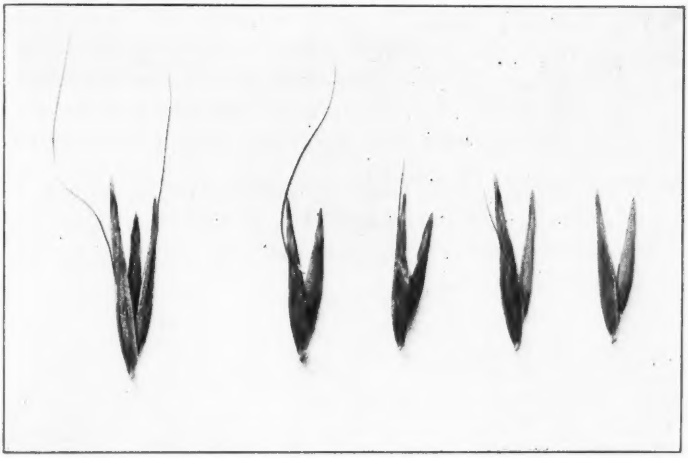

FIG. 2. Showing gradations in the weak-awn series, from a spikelet having two weak awns down to the awnless type.

therefore, to one representative panicle from each plant. The spikelets were picked from such a panicle, examined for awns, and placed in a small seed envelope on which was recorded the data as to total number of spikelets, number with one awn, and number with two awns.

MATERIAL

The weak-awned varieties reported on here are the Burt and a strain of the Red Texas. Attention was centered upon the variety Burt. The awnless type in all cases was the cultivated variety Sixty-Day. For the strong-awned oat, a strain of *Avena fatua* was used. All forms had been grown in pure line culture previous to crossing and were uniform within themselves.

Series 514a1 — Burt × Sixty-Day

(Weak Awn × Awnless)

A cross between the Burt and Sixty-Day gave an F_1 which was almost awnless. A few plants had awns on some of the spikelets, but the generation could be considered practically awnless.

The second generation plants showed all degrees of awning, from the perfectly awnless condition to those which were one hundred per cent. awned like the Burt parent. These F_2 individuals were first grouped according to percentage of awned spikelets, with a class range of ten per cent. (Table I.)

TABLE I

F_2 OF 514A1[2]

Per Cent. of Awning	f
0	110
1–10	29
11–20	23
21–30	25
31–40	18
41–50	18
51–60	14
61–70	8
71–80	12
81–90	5
91–99	12
100	66

The occurrence of plants having varying percentages of awned spikelets and forming a more or less continuous series between the parental types, at first suggested a multiple factor condition for awning. A study of the frequencies, however, showed that such an assumption was incorrect. The frequencies of the zero and 100 per cent. classes were too high to accord with an hypothesis of this sort.

When the F_2 plants were grouped in the classes—awnless, partially awned, and fully awned, it was seen that the data approached, in a general way, a ratio of 1:2:1. (See Table II.) The ratio of the first two named classes to the third was found to be 4.15:1, or, on a basis of four, 3.22:.78.

It remained for a study of the F_3 material, however, to throw light upon the number of factors concerned in this cross, and the relation of these factors to each other.

[2] It was necessary to reduce the class range in the case of the 91–99 class, in order to provide the 100 per cent. class. This, however, could have no effect on the conclusions drawn from this table.

TABLE II

F_2 OF 514A1

Awnless	110	274
Partially awned	164	
Fully awned	66	66
	340	340

Behavior of the Fully-awned F_2 Plants.—Seed of three of the fully-awned F_2 plants was sown in pedigree culture for an F_3. The results obtained are shown in Table III.

TABLE III

F_3 FROM FULLY AWNED F_2 PLANTS—514A1

Pedigree	% Awns in F_2	Awnless	Partially Awned	Fully Awned
514a1–22	100	0	0	47
514a1–88	100	0	0	36
514a1–95	100	0	0	20
Total	...	0	0	103

From this data, it would appear that the fully-awned type is the pure recessive. We have already seen that this type has very little influence on the F_1 hybrid, and that it appears in F_2 in only about 25 per cent. of the individuals. Here we find the fully-awned plants breeding true.

Behavior of the Partially-awned F_2 Plants.—Twelve plants which showed some awning in the second generation were planted in pedigree rows for F_3. The percentage of awning in these plants varied from eleven to eighty-seven. In spite of the wide difference as to percentage of awning, their behavior was strikingly similar. With but one or two exceptions, the ratio of plants not fully awned to those which were fully awned was close to 3:1. A total of all these F_3 plants gave the frequencies 419:118, or a ratio of 3.12:.88. In this case the deviation is 2.4 times as great as the probable error, but this can be accounted for by the somewhat wide deviations occurring in cultures 106 and 194. With the exception of these pedigrees, the deviations from the expectancy are not more than twice the probable error. It is of

interest to note that plants with a high percentage of awned spikelets in F_2 did not tend to give a correspondingly high number of awned plants in F_3. Neither did plants with a low percentage of awns in F_2 tend to produce more of the awnless or partially-awned types in F_3.

TABLE IV

F_3 FROM PARTIALLY AWNED F_2 PLANTS—514a1

Pedigree	Per Cent. Awns in F_2	Awnless	Partially Awned	Fully Awned	Not Fully Awned	Fully Awned	Ratio $\times 4$	D	P.E.	D/P.E.
514a1– 55	77	13	16	11	29	11	2.90 1.10	.10	.185	.54
–100	24	36	17	19	53	19	2.94 1.06	.06	.137	.44
–106	11	31	7	5	38	5	3.54 .46	.54	.178	3.03
–119	20	17	8	11	25	11	2.78 1.22	.22	.195	1.13
–128	87	24	11	12	35	12	2.98 1.02	.02	.171	.12
–138	32	13	15	5	28	5	3.39 .61	.39	.203	1.92
–172	15	26	6	8	32	8	3.20 .80	.20	.185	1.08
–194	14	36	19	11	55	11	3.33 .67	.33	.144	2.29
–200	18	24	12	11	36	11	3.06 .94	.06	.171	.35
–216	30	11	18	8	29	8	3.13 .87	.13	.192	.67
–244	60	13	17	7	30	7	3.24 .76	.24	.192	1.24
–264	81	23	6	10	29	10	2.97 1.03	.03	.187	.16
		267	152	118	419	118	3.12 .88	.12	.05	2.40

Behavior of the Awnless F_2 Plants.—Eleven of the awnless F_2 plants were selected for study in F_3, and seed from them was sown in short pedigree rows. The behavior of these plants is shown in Table V. Five of these awnless plants bred true to the awnless condition, giving a total of 249 awnless plants in F_3. The other six broke up into awnless, partially-awned, and fully-awned plants. In no case did the ratio of these types suggest a 1:2:1 ratio. When we group all of the plants which are not one hundred per cent. awned, however, and compare them

with the fully-awned plants, we find that the separate ratios closely approximate a 3:1 ratio. The ratio for all six plants is 2.97:1.03, and its deviation is practically the same as its probable error.

TABLE V

F_3 FROM AWNLESS F_2 PLANTS—514A1

Pedigree	Per Cent. Awns in F_2	Awnless	Partially Awned	Fully Awned	Not Fully Awned	Fully Awned	Ratio ×4	D	P.E.	D/P.E.
514a1– 34	0	48	0	0	48	0				
–126	0	75	0	0	75	0				
–185	0	31	0	0	31	0				
–336	0	32	0	0	32	0				
–232	0	63	0	0	63	0				
Total	..	249	..	..	249	..				
514a1–339	0	34	0	8	34	8	3.24 .76	.24	.180	1.33
– 36	0	52	3	15	55	15	3.14 .86	.14	.140	1.00
–176	0	26	6	11	32	11	2.98 1.02	.02	.178	.11
–221	0	11	4	7	15	7	2.73 1.27	.27	.249	1.08
–247	0	18	7	15	25	15	2.5 1.5	.5	.185	2.70
–291	0	29	3	11	32	11	2.98 1.02	.02	.178	.11
Total	..	170	23	67	193	67	2.97 1.03	.03	.072	.43

It is apparent from these data that the F_2 grouping used here includes in the awnless class certain individuals which are heterozygous for awning, and which really belong with the partially-awned plants. According to Nilsson-Ehle (1914) environmental conditions have an effect upon the production of awns. It is quite possible that the failure of these six plants to produce some awns is due to undetermined environmental factors.

A comparison of the relative numbers of awnless and partially-awned plants in Tables IV and V would seem to indicate that awnless F_2 plants tend to give a higher percentage of awnless plants in F_3 than do the partially-awned plants. This may be explained, however, by the

fact that a high percentage of the awnless plants in the second generation were yellow in color and consequently many of them might well carry a factor which inhibits awn formation. Data will later be presented to show a definite linkage between the awn-inhibiting factor and the factor for yellow color in the Sixty-Day.

Series 2501a1 — Burt × Sixty-Day

A second series of hybrids between Burt and Sixty-Day behaved in a manner similar to series 514a1. The F_1 was nearly awnless in both the direct and reciprocal crosses. The F_2 results are shown in Table VI.

TABLE VI

F_2 OF 2501

Pedigree	Awnless	Partially Awned	Fully Awned	Not Fully Awned	Fully Awned	Ratio ×4	D	P.E.	D/P.E.
2501b1	26	96	43	122	43	2.96 1.04	.04	.0909	.44
2501ar1	17	61	28	78	28	2.94 1.06	.06	.1134	.53
2501ar2	4	32	17	36	17	2.72 1.28	.28	.1604	1.75
2501ar3	1	11	4	12	4	3.00 1.00	.00	.2921	0.00
Total	48	200	92	248	92	2.92 1.08	.08	.0634	1.26

2501b1 = Burt X Sixty-Day.
2501ar1 = Sixty-Day X Burt—selection of partially awned F_1 plants.
2501ar2 = Sixty-Day X Burt—selection of awnless F_1 plants.
2501ar3 = Sixty-Day X Burt—unselected F_1.

It will be seen from Table VI that the partially-awned and awnless types of F_1 gave practically the same behavior, each throwing about 25 per cent. of fully-awned plants in F_2.

Series 2401a1 — Red Texas × Sixty-Day

A cross between Red Texas (weakly awned) and Sixty-Day gave an F_1 showing only 1.3 per cent. of awning. The second generation of this cross has not yet been grown.

Discussion of Results in Weak-awn × Awnless.—From the data presented above, the following conclusions may be drawn as to the inheritance of awns in crosses between the weak-awned and the awnless types of oats.

The awnless type is almost completely dominant in the first generation, only a few of the plants possessing awns and those in small percentages.

The second generation gives awnless, partially-awned and fully-awned plants in a ratio which approximates 1:2:1. The totals of data from second generation plants of series 2,501 and 514 are reasonably close to this ratio:

	Awnless	Partially Awned	Fully Awned
Series 2501	110	164	66
Series 514	48	200	92
Total	158	364	158
Expectancy	170	340	170

The behavior of the fully-awned plants shows that this type is the pure recessive, for it breeds true in all cases from the second generation.

All of the partially-awned F_2 plants proved to be heterozygous, throwing in the third generation approximately three plants not fully awned to one fully-awned plant.

The awnless plants of the second generation were found to comprise both homozygous plants of the parental type and heterozygous intermediates which later broke up in the same manner as the partially-awned F_2 plants. It might be expected that some of the awnless F_2 plants would prove to be heterozygous, since awnless plants are found commonly in the first generation.

From these results, it is apparent that we cannot correctly speak of the awnless oat as the dominant type, nor should we restrict the use of the term intermediates to those plants which are partially awned.

It seems very probable that the difference between the weak-awned and the awnless varieties of oats, at least in the varieties studied, may be accounted for by the assump-

tion of a difference in one pair of genetic factors. It may be that awnlessness is a definite character which is a true allelomorph of the fully-awned condition. Some might prefer, however, to consider awnlessness simply as the absence of awning. In that case we must assume the presence of an inhibitory factor to account for the partial dominance of the awnless Sixty-Day over the weak-awned Burt. The data at hand seem to point to the presence of an inhibitor to awning in the variety Sixty-Day. A preponderance of awnless yellows in F_2 and F_3 suggests a linkage of this inhibitory factor with the factor for yellow color in the Sixty-Day. (See Table VII.) Such a finding would be in agreement with the results of Nilsson-Ehle (1914). A very definite linkage of the inhibitory factor with the factor for yellow color has already been observed in a cross between *A. fatua* and *A. sativa* var. Sixty-Day. This will be brought out in a later publication.

TABLE VII

SHOWING THE DISTRIBUTION OF REDS AND YELLOWS IN SERIES 514, WITH PERCENTAGE OF AWNING AS RELATIVE[3]

	0	5	15	25	35	45	55	65	75	85	95	100
Red.....	49	12	10	12	12	8	10	5	8	5	7	38
Yellow...	50	15	12	12	4	10	4	2	2	0	4	21

Certain other crosses with the Burt show that this variety contains a factor for yellow which does not inhibit awning. In the crosses Burt (red) $\times$ Swedish Select (white), and Burt $\times$ Early Champion (white), the F_2 contained a certain number of yellow-seeded plants, which in turn gave some yellows in F_3. All of these yellows were fully awned. The existence of this yellow factor in the variety Burt has complicated the study of the yellow of the Sixty-Day in these crosses . The fact of the presence of this yellow in the variety Burt should be kept in mind when Table VII is examined.

It will be seen in Table VII, that the red grains are nearly as numerous in the 100 per cent. class as in the

[3] The classes are as follows: –0, 1–10, 11–20, ..., 91–99, –100.

awnless class, and that the other classes are represented in practically equal numbers. In the case of the yellows, however, there are about two and one half times as many in the awnless class as in the fully-awned class. Fifty-seven per cent. of the yellows have less than 20 per cent. of awning, and seventy-three per cent. have less than 30 per cent. of awning. Many of the yellows in the 100 per cent. class are doubtless due to the yellow factor contained in the Burt parent. This factor does not inhibit awning.

Strong Awn × *Awnless.*—The results of crosses between *Avena fatua* and the variety Sixty-Day (*A. sativa*) agree closely with those obtained in the crosses between the weak-awned and awnless types. (See Tables VIII and IX.)

TABLE VIII

F_2 TOTAL OF SERIES 2516

Pedigree	Awnless	Partly Awned	Fully Awned	Not Fully Awned	Fully Awned	Ratio × 4	D	P.E.	D/P.E.
2516	169	377	201	546	201	2.92 1.08	.08	.04	2.00

TABLE IX

F_3 OF HETEROZYGOUS F_2 PLANTS

Pedigree	Awnless	Partly Awned	Fully Awned	Not Fully Awned	Fully Awned	Ratio × 4	D	P.E.	D/P.E.
687a1–15	61	124	67	185	67	2.94 1.06	.06	.07	.86
687a1–5	79	53	41	132	41	3.05 .95	.05	.089	.56
687a1–1	15	55	24	70	24	2.98 1.02	.02	.12	.17

In a similar study on *A. fatua* × *A. sativa* var. Kherson, Surface (1916) obtained results which agree closely with those presented above. The F_1 plants were nearly intermediate, although "The majority of F_1 spikelets show no awn whatever" (p. 265). In the second generation the following types appeared:

Awnless	133
Intermediate	215
Wild (fully awned)	112

At first Surface assumed that the awnless plants were homozygous and should, therefore, breed true. A test of these plants, however, showed that a certain number were heterozygous. Fifteen out of twenty broke up in the third generation. This might be expected from the fact that some of the heterozygous F_1 plants were awnless. The failure of these plants to produce a few awns is attributed by Surface either to an undiscovered factor affecting awning, or to an environmental influence. It seems quite probable that the variety Kherson may carry a factor inhibitory to awning, similar to the factor in the Sixty-Day.[4]

OTHER CHARACTERS OF THE GRAIN

In connection with the above studies on awning, studies were also made on the presence of basal hairs and the type of articulation of the lower kernel of the spikelet. A strong correlation was found to exist between the fully awned condition and the Burt type (similar to that of *A. sterilis*) of articulation, and also between the fully-awned condition and the presence of medium-long basal hairs such as are found on the Burt grains. When the spikelets were all awnless, the union of the lower kernel and its rachilla was generally of the type found in *Avena sativa* and the basal hairs were either short or lacking.

It is interesting to note, in the crosses between the weak-awned and awnless types, that in every case where a panicle had two awns on a spikelet, all of the spikelets on the panicle were awned. The irregular occurrence of these two-awned spikelets, and the wide variability in numbers on a panicle, makes it seem probable that there is no definite factor for the two-awned condition. It seems more likely that the occurrence of such spikelets is due to environmental influences upon the factor for complete awning.

[4] In some localities the names *Kherson* and *Sixty-Day* are used synonymously.

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SHORTER ARTICLES AND DISCUSSION

NOTES ON THE FAUNA OF GREAT SALT LAKE

In the years during which the writer was zoologist at the University of Utah (1908–15) observations were made on the life of the Great Salt Lake, when time could be spared from multitudinous teaching duties. The animals of this brine lake earliest reported, *Artemia fertilis* Verrill, and the larvæ of the small Dipteron, *Ephydra gracilis* Packard, were naturally the first attraction, since they were abundant, commonly known to science, and readily observable to any one looking for them. A second species of *Ephydra, E. hians* Say, was reported by Aldrich in 1912.[1] A *Chironomus* has been reported also, according to Talmage,[2] but no reference to the authority is given and his own statement is confusing, as he says he has "confirmed the presence of . . . the larvæ of one of the Tipulidæ, probably *Chironomus oceanicus* Packard"! He further states that "The larvæ of the tipula may be taken anywhere near shore during the warm months," but the present writer is compelled to state that neither larvæ, pupæ or adults of either a Tipulid, or of a *Chironomus* was ever observed by him in the Lake, nor are any such reported by Aldrich, an authority on Diptera, in his reports of collecting about Great Salt Lake.[1, 3] Other forms than *Ephydra* might well occur in such a portion of the lake as the great Bear River Bay, where the salt content of the water must be much less, owing to a great influx of fresh water from the Bear River, and to the fact that the bay is partially cut off from the main lake by the causeway of the Southern Pacific Railway. Aldrich, however, has certainly been on the Bear River Bay side of the cut-off, as shown by Plate II, Fig. 8.[1]

In tentatively "trying out" to see what might be a profitable line of study several dilutions were made in order to note the

[1] Aldrich, J. M., "The Biology of Some Western Species of the Dipterous Genus *Ephydra*," *Jour. N. Y. Ent. Soc.*, XX, 77–99. In this are photographs indicating the enormous numbers of *Ephydra* in the lake; also first complete description of *E. gracilis*.

[2] Talmage, J. E., 1900, "The Great Salt Lake, Present and Past," 67–68.

[3] Aldrich, J. M., "Collecting Notes from the Great Basin and Adjoining Territory (Dipt., Col.)," *Ent. News*, XXIV, 214–221.

effect, if any, on *Artemia*. The brine varied in density in the lake at Saltair during the years of these observations, according to season and rainfall, and besides the annual fluctuations gradually became less dense on account of a cyclical period of heavier precipitation and consequent rise in level of the lake. In October, 1909, the density was 1.158, and in April, 1915, 1.136. Dilutions were made by addition of distilled water as nearly as was feasible to the following densities: 1.12, 1.10, 1.08, 1.06, 1.04, 1.02, 1.01[4] These dilutions were placed in small aquarium jars, filled only ¼ to ½ full, and covered to prevent entrance of dust, and undue evaporation. It may be said at once that while Schmankewitsch's classic observations on *Artemia* were of course in mind, it was not hoped to repeat them with the small amounts of water used. However, some data obtained, though incomplete, seems worth recording, since the present writer can scarcely hope ever to have further opportunity for pursuing this line of investigation to the extent it deserves. It is sincerely hoped that some one may be able to further investigate the fauna normal to the unusual ecological conditions of brine lakes.

Resistance of the adult *Artemias* to sudden changes in the concentration of the salts, while greater than anticipated, only showed that they could not indefinitely survive too great a change. Plunged into tap water, they appeared "heavy," sinking at once to the bottom, from which with most vigorous swimming movements they were barely able to rise. Exact data as to length of life in these solutions is not sufficient to offer, but in general they survive a change to completely fresh water but a few hours, and they do not survive for long periods in water in which the amount of salts has been reduced to less than half the normal. In stronger concentrations they survive for sufficiently long periods that it seems likely they would live therein for a normal life period if other conditions were favorable. Kellogg[5] had opportunity in the case of *A. franciscana* Kellogg to note differences in size, color and abundance of individuals which had developed in waters of different densities, and it is interesting to note that he found them largest in waters ranging from 1.11 to 1.13 in density. The latter figure is nearly the same as

[4] See article by Daines preceding this, with exact densities of one series. Part of these observations were made in collaboration with Daines.

[5] Kellogg, V. L., "A New *Artemia* and its Life Conditions," *Science*, N. S., XXIV, pp. 594–596.

that for Great Salt Lake water at the beginning of my observations, at which time the lake was in the rising period of its long cycle of rise and fall, which rise continued at least up to 1915. Some few years prior to 1909 the lake had been much lower and the water at nearly the saturation point for NaCl. I believe 1.13 is somewhere near the mean density for Great Salt Lake.

Interesting facts were noted concerning eggs contained in dilutions made in autumn (see annual cycle below). These hatched in a few days or weeks, and they first hatched in the most dilute water, next in the next more concentrated, and so on up the scale of concentration in nearly regular order. The conclusion naturally presents itself that the stimulus to development lies in the reduction in amount of salts present, but later it appeared (this point was not finally cleared up) that it lay rather in a lack of oxygen resulting from insufficient aeration of the water used. Young thus hatched never reached maturity.

Ephydra larvæ are even more abundant in the lake than *Artemias*. They were found to be remarkably resistant to changes in density of water, as well as to other changes in liquid environment. These larvæ will live at least for days in tap water, but whether they could be brought to maturity in this or in very dilute lake water was not determined. The fact that the puparia drift up on shore in great "windrows" has already been noted by Aldrich,[1] and in the *Canadian Entomologist* for 1891 (original article not seen). The countless swarms of imagoes may be seen by bathers resting on the surface of the water or flying up at will, and it was found to be an easy matter to obtain the eggs by imprisoning a number of these in a covered crystallization dish with clean bottom, partly filled with brine, showing, as suspected, that they drop the eggs freely into the water. As this was not done until near the close of my service in Utah, no experiments were made with the eggs, but attempts to hatch the eggs and rear the insects to the imago stage in dilute lake water and in fresh water should be made. As instances of the resistance of these larvæ may be mentioned the following: In more than one case the larvæ were observed to live months in brine which had evaporated to saturation, and beyond to the point of containing a heavy deposit of crystals and of being completely encrusted on top, and in one such case practically all of the water had disappeared. Among the salt crystals in the little remaining water the larvæ were somewhat inactive, but appeared to be in good condition when water to about the normal amount

was restored to the jar. *Artemia* is resistant to concentration, but not to the same degree as *Ephydra* larvæ. Again, in an attempt to kill larvæ without distortion some were placed in Perenyi's fluid and in this were capable of movement after more than twenty-four hours. In Flemming's fluid they live several times as long as *Artemia,* but I have no record of the exact length of time. I am able to verify with certainty Aldrich's belief that these larvæ do not rise to the surface for air.

Most important of the incomplete observations were those indicating the presence of Protozoa as normal inhabitants of Great Salt Lake. So far as I am aware, no Protozoa have been previously reported from brine lakes. Representatives of this group, notably *Amœbæ,* were first seen in the moderate dilutions after some weeks in the laboratory, which proved to be in a sense cultures. In March, 1910, several jars of a series, including one of undiluted lake water, contained an abundance of these forms. The specimens were of two or three varieties or species, by far the most common being very like *Amœba limax.* I should not have hesitated to call it that in a fresh-water culture. A class of some 15 students was well supplied with *Amœbæ* for laboratory work from one of these jars. Occasionally, in making microscopic examinations of the cultures other Protozoa were met with, but never in numbers. In fact only a single specimen at a time was the rule. Specimens of Ciliata were seen, some closely resembling a species of *Uroleptus,* while at least once a species of *Euglena* was definitely noted. *Chlamydomonas* appeared quite regularly and in great quantity in many of the cultures.[4] I believe several species of Protozoa to be present normally in the Great Salt Lake, but not generally very abundant, as many of my efforts to secure them directly from the lake were failures. However, some were certainly obtained directly from the more or less decayed masses of organic débris which collect in enormous quantity in the great stretches of shallow water along the very flat shore, which masses consist mainly of the gelatinous blue-green alga, *Aphanothece packardii.*[4] (This is the alga "of the *Nostoc* group" mentioned by Aldrich.) In this material it was expected there might be found Nematodes, as they are in so many cases adapted to unusual environment, and so commonly present in decaying substance, but none ever came under observation.

Perhaps a statement of the annual cycle of life of *Artemia* and *Ephydra* may be of interest. For the latter it may be said that

larvæ and pupæ are at all times of the year present in the lake, though less abundant in winter. In the winter months there are but few in the open water, but they are common in the débris above mentioned. Dates for first appearance of adults were not secured, though some appear as early as April; they become common by June, and in July and August are so exceedingly numerous as to be a serious nuisance at times about Saltair pavilion, wind conditions being apparently a determining factor in their coming in swarms about the bathhouses. Ordinarily they keep below the level of the floors, on the piles and on the water surface. Whether any eggs survive the winter can not be stated. There is no evidence of the pupæ surviving on shore, where thrown up by the waves. It seems likely that larvæ and pupæ which remain submerged are the principal, if not the sole means of surviving the winter period.

Adult *Artemias*, the females with fully developed egg sacs, are very plentiful throughout the summer and fall into October. In this month the temperature of the water falls from the summer temperatures of between 25° and 30° C. (exact summer maximum unknown to writer) to as low as 15°–18° C. In November with the temperature as low as 6° C. there may still be seen some few adults. At a December temperature of 1° C. and lower (doubtless goes lower at times for short periods) no adults can be found, as a rule, though reported by Talmage. An abundance of eggs can be secured in fall, winter and spring, especially in the débris near shore. Possibly some may settle into the smooth oolithic sand of the open lake bottom, but I have no evidence that such is the case, and the eggs tend rather to float than to sink. Young appear in April and May, abundantly in the latter month. The earliest record secured for young was March 12 (1910), when a number of minute young were taken. The temperature at that time was 9° C. It will be noticed that *Artemia* differs markedly in its long season of activity from its fresh-water cousin, *Branchipus*, which is so soon gone from its evanescent breeding pools. Correlated with this long active period is the continued presence of abundant water and food and an entire absence of enemies. Enemies play no part in keeping down the numbers of *Artemia*, or of *Ephydra* in the larval stage. In the midsummer bathing season both are present in myriads in the open water, but so transparent are they that the average bather, even the native Salt Laker, seldom notes their presence.

The insect fauna of the lake shore presents material for a study in itself, on which nothing has been published save the material on Diptera by Aldrich, already cited. At the University of Utah I left the beginning of a collection of insects taken in or on the waters of the lake, and I recall that a small Corisid was several times seen and some specimens of it taken swimming immersed in the brine near shore. The species appeared to be the same as one common in fresh and slightly salt and sulphur impregnated waters in the Salt Lake valley.

Probably correlated with the abundance of *Ephydra* adults as food, may be mentioned a "plague of spiders" with which the resort (Saltair) was troubled during one bathing season, about 1910. Several cases of persons being bitten by spiders were reported in one of the Salt Lake papers, though I can not vouch for their authenticity. Certain it is that spiders of more than one species were unusually numerous about the pavilion, as I personally observed, and I learned later that the employees went about with brooms every morning before the hour for opening and destroyed as many as possible. The forest of piles and underpinning beneath the structure, however, was an inexhaustible reservoir from which the supply was constantly renewed. After the close of the season, no other remedy having been found, some employees were kept busy for weeks in boats beneath the huge structure collecting and destroying the egg cocoons, and the next season there was no serious trouble. Many bushels were thus collected. The second autumn this task was again taken up, and since that time no further plague of spiders has appeared, but whether autumn cocoon collecting is still kept up I do not know. I have no doubt that the seemingly sudden appearance of the great numbers of spiders was in reality but the time when, owing to the availability of a great food supply and plenty of space for spreading webs, they reached a high point in numbers, the culmination of years of slow increase.

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ON THE FLORA OF GREAT SALT LAKE

VERY little investigation has been made of the plant life of Great Salt Lake, either of a scientific nature or otherwise. So far as the author of this paper knows, but one attempt has been made in the past so scientifically classify the flora of the lake, and

that attempt was interrupted before it had reached a successful conclusion, so that no publication of the work was made.

Brief mention of what literature we have on this subject seems not to be out of place here.

Professor Farlow (1879)[1] published a description of a blue-green alga, *Polycystis packardii.*

Dr. A. Rothpletz (1892)[2] makes mention of the presence of certain genera of blue-green algæ, connecting them with the formation of peculiar ooliths on shore. Dr. Rothpletz did his work as a geologist, from a geological point of view. He made no systematic study of the lake from a botanical standpoint. The genera of algæ he mentions—*Gleothece* and *Gleocystis*—we have been unable to find in the part of the lake studied, and it might be said, too, that the connection between these and the ooliths has not been generally accepted, even by geologists.

H. F. Moore (1899)[3], in reporting on the feasibility of introducing useful marine animals into the waters of the lake, makes mention, briefly, of the presence of diatoms. As diatoms constitute the chief food of the oyster, their presence was of considerable importance in the investigation, and especially since they are found in greatest abundance at the mouths of rivers where the density of the water is more favorable for the development of the oyster.

Talmage (1900)[4] speaks of the presence of at least three species of algæ—not naming them—and, besides these, he calls attention to the presence of diatoms beds off from shore, as well as living diatoms in the lake.

Miss Tilden published in her distribution entitled "American Algæ," several species from Great Salt Lake. This distribution has not been available, therefore, more definite mention of it can not be made. They are as follows:

Aphanothece utahensis, no. 297,
Polycystis packardii, no. 298,
Dichothrix utahensis, no. 288,
Enteromorpha marginata, no. 266,
Enteromorpha tubulosa, no. 262,
Chara contraria, no. 255.

No other proof of the presence of abundant plant life in the

[1] This paper was not available.

[2] Rothpletz, A., *Bot. Centr.*, p. 35.

[3] Moore, H. F., "The Feasibility of Introducing Useful Marine Animals into the Waters of Great Salt Lake."

lake is needed than the presence of a fauna, abundant in individuals, if not in species. And no further demonstration of the presence of this fauna is required than for one to visit the lake and see, with his own eyes, the water literally teeming with animal life.

The presence of plants is not so evident to the casual observer, although, at certain times of the year, clumps of greenish material, which must at least suggest a vegetable growth, are very plentiful. Areas of a green scum on the surface of the water in more or less protected places also give evidence, directly, of the presence of plants.

The original purpose of this paper was to determine, if possible, the effect as to size of cells and rapidity of growth of different densities of Great Salt Lake water on a species of *Chlamydomonas* which is found there. The problem, then, was to have been purely a physiological one. During the course of investigations along this line, however, other interesting things presented themselves, and a deviation was made from the first plan, so that finally observations were extended to include every species of plant found in the part of the lake investigated.

The observations made covered a small portion of the southern end of the lake at what is known as Saltair Beach. This place is easily accessible, and is at such a distance from any stream entering the lake, that the density of the water there is not affected to any degree.

The following plants are found regularly in the water at that place:

A green alga, *Chlamydomonas* sp., which has been examined by Dr. N. L. Gardner. Dr. Gardner believes it to be a new species —he has not yet published a decription—near to *Chlamydomonas glœocystiformis* Dill, and *Chlamydomonas apiocystiformis artari.* It has a rich green color, and occurs, during the warmer weather, on the surface of the water in many more protected places. It is found in less numbers in whatever decaying plant or animal material may be present. The indications are that this is one of the means the plant has of surviving the winter; since such material brought into the laboratory in the very coldest weather has later developed a rich green growth of the alga.

A blue-green alga, determination of which has been made by Professor W. A. Setchell. He says that it certainly is an *Aphanotheca,* and is undoubtedly the same plant as the one named *Polycystis packardii* by Farlow, and probably also the

same as the one distributed by Miss Tilden from the Great Salt Lake and named by her *Aphanothece utahensis*. On the authority of Professor Setchell, we shall designate it *Aphanothece packardii*.

The plant occurs in small masses, irregular in size, floating in the water and piled up by the waves on shore. These masses show a gradation in color from a deep blue-green, to light brown, and some were colorless; this depending, no doubt, on the conditions of the plants in the individual clumps, and not, as has been suggested,[4] on a variety of species in the clumps. Microscopic examination of this material shows the individual plants in the mature condition, and also in various stages of division by fission. Great numbers of the cells are held together by their gelatinous secretions. The individual plants average about two micra in diameter.

Microscopic examination of the lake water reveals at least two species of diatoms. They probably belong to the genera *Navicula* and *Cymbella*. These plants do not occur in sufficient numbers, in the denser water about Saltair, to be seen with the naked eye.

The fact that putrefaction and decay are taking place in the water, especially near to shore, where organic material is abundant, shows conclusively that bacteria are present.

Here it may be well to suggest that at least some of the plants distributed by Miss Tilden as Great Salt Lake plants, in all probability came from the fresher waters at and near the mouths of rivers, or in the bays formed by the rivers at their place of entrance into the lake. As the present observations were confined to the denser waters, even an indication of the plants referred to—with the one exception noted—was not found.

For the physiological work, water was transferred from the lake to the laboratory, in sufficient amount to make a number of series of dilutions in glass aquaria. These series included solutions of different density, varying in specific gravity from 1.0115 to 1.222, a saturated solution.

Masses—large in some series, but small in one—of *Aphanothece packardii* were placed in these solutions, and, in every case, enough *Chlamydomonas* was thus introduced to start a more or less flourishing growth.

From time to time, measurements were made of the *Chlamydomonas* present in the solutions, and during the first few

[4] Talmage, J. E., "The Great Salt Lake—Present and Past," p. 76. Salt Lake City.

months indications pointed very strongly to the fact that a reduction in size followed transplanting into less dense solutions.

A table below shows the results obtained with the first series. No. 1 contains the water as obtained from the lake, analysis of a sample of which (1910)[5] gives the following:

Constituents	Grams per Liter	% of Sample Taken	% of Total Solids
Total solids	242.25	20.887	——
Chlorine	126.35	10.91	52.23
SO_4-radical	16.00	1.38	6.65
Magnesium	5.18	0.45	2.14
Calcium	0.98	0.08	0.39
Sodium	85.10	7.25	31.68
Potassium	8.82	0.76	3.66
Total of constituents	242.45	20.83	99.75
Salinity	213.32	18.39	88.09

Solutions 0 and 00 were allowed to become further concentrated by evaporation in the laboratory. Nos. 2 to 8, inclusive, were diluted with distilled water. The first measurements were made some time after the series was started to allow the plants to become accustomed to the new conditions, only, indeed, after multiplication had begun. Blank spaces in the table indicate that no motile zoospores were present at that time in the solution.

SERIES NO. 1 STARTED OCTOBER 8

Measurements

No. of Solution	Density	Dec. 15	Jan. 13	Feb. 14	Mar. 10	Apr. 16	June 15	Average
00	1.222				11.7×6.7		15×10	13.3×8.3
0	1.1825	13×7					15×10	13.7×7.8
1	1.1580	13×7.25	12× .5	13×6.5	12×5.4	12×6	12× 7	12.2×6.1
2	1.1239	13×5			11×5	11×6	10× 5	11.2×5.2
3	1.1088	12×5	11×5		11.2×4.5	11×6	9× 5	10.8×5.1
4	1.0822	12.5×5		12×6.5	11.25×5.5	10×5.5		11.4×5.6
5	1.0613		11×4.3			10×5.5	10× 5	10.3×4.9
6	1.0400	9×4.5		9×5	9×5.5	10×5		9.25×5
7	1.0190		8.5×5		9×4.5	8.5×4.5		8.7×5
8	1.0115				11×6.5	10×5	10× 6	10.3×5.8

This table seems to show a slight diminution in size as we pass from the more dense to the less dense solutions, with the exception of the last and least dense of the solutions. It must be said that it is very difficult in measuring *Chlamydomonas* zoospores

[5] McFarlane, Wallace, "The Water of the Great Salt Lake." (Read before the summer meeting (1910) of the Am. Chem. Soc. at San Francisco by Professor W. C. Ebaugh.)

to make definite comparisons as to size. The size of the individual cells even in one solution varies so greatly that one can only obtain an average of the size and then very roughly. The measurements recorded in the table, and all others made, represent the average size of the larger cells in the solutions as far as it was possible under the circumstances to measure them.

The results from the other series did not corroborate definitely the results shown for the first series. Therefore, the only conclusion which can be drawn is, that so far as the present work has shown, variations in density of the water of Great Salt Lake cause no corresponding variations in size of *Chlamydomonas* cells.

In every series but one, decided growth of the *Chlamydomonas* began first in the dilutions about No. 5, and appeared then in order up to No. 1, No. 0, and No. 00, and then down from No. 6 to No. 8. Solutions No. 4, No. 3, and No. 2, as a rule, showed a greater abundance of the zoospores, judging from depth of the green color given to the solutions by them.

The indication is, that water somewhat less dense than that normally present in the lake at its present level is most favorable to development of *Chlamydomonas* sp.

Aphanothece packardii does not grow well in the laboratory cultures. It was interesting to note that they lost their blue-green color and died in the weakest solutions first; this condition following regularly up the series to the most dense solutions. This species gave us no further results. Whether this failure was due to the weak solutions being particularly unfavorable to the alga, or whether it merely indicates that this form is difficult to keep under laboratory conditions, is not certain. The latter seems the more likely conclusion.

The diatoms recovered from the dense waters, on being transferred to the weaker solutions in the laboratory, multiply readily and actually thrive, giving large masses of the characteristic brown growth. In every series, after about a month in the laboratory, solutions No. 1 and No. 2 show a very few live forms which soon die. In No. 3 a few persist; but in No. 4, No. 5, No. 6, and No. 7, they appear abundantly and continue to multiply indefinitely. In No. 8 the live plants are again not very numerous. These observations are in complete harmony with the statements[3] that the diatoms are found in great abundance in the shoaler, fresher waters near to the mouths of the rivers emptying into the lake. They are reported to be especially numerous on

the alluvial fans at the mouths of both the Bear and the Jordan rivers.[3]

The results seem to indicate that the diatoms obtained are true Salt Lake forms, but have become adapted to less severe conditions than prevail in the denser waters. That they are not fresh-water forms which have accidentally found their way into the lake, is suggested by the fact that they do not thrive in the least dense of the solutions of any of the series.

In every series, a cloudiness in the solution appeared as a result of bacterial growth, but the order of appearance in every case was from the least dense solutions up to the most dense. This cloudiness soon disappeared, to reappear at irregular intervals. These facts led to an attempt to determine at least the number of species of bacteria which may be found in the part of the lake studied. So far as we can determine, no attention whatever has been given this phase of the question in the past.

Five distinct organisms, which have adapted themselves to conditions there, were isolated in pure cultures. No detailed study was made of them to determine their species, but enough was done to leave no doubt as to their being at least separate varieties, if one may judge from distinct differences in cultural and morphological characteristics.

Water obtained from the lake under the strictest precautions, was at first plated on phosphorescent, or salt agar, which consists of 40 cc. of normal sodium hydroxide and 25 grams sodium chloride, to 1,000 cc. of plain agar. Later samples of the water were plated on gelatins containing different amounts of the normal NaOH, and NaCl. Better results were obtained with the salt agar than with the gelatin. Later, plain agar was used with good results.

The number of bacteria per c.c. varies between 200 and 625, counts having been made from a number of samples taken in the coldest weather—water 33° F.—as well as in the warmer weather.

A very interesting fact developed; that of the five micro-organisms isolated, three are decided chromogens, each producing abundant pigment. Of the five, one is a diplococcus, which appears sometimes in tetrads and singly. It forms large white colonies on the media used. The other four are bacilli. The one producing no pigment, forms delicate white colonies on the solid media. Of the chromogens, one produces a lemon-yellow; a second produces a bright orange; and the third produces a violet pigment.

CONCLUSIONS

1. Variations in density of the water of Great Salt Lake, cause no corresponding variations in the size of *Chlamydomonas* sp. cells.

2. The indication is, that water somewhat less dense than that normally present in the lake, at its present level, is most favorable to the development of *Chlamydomonas* sp.

3. The diatoms present in the lake multiply best in water much less dense than the dense water at Saltair.

4. At least four species of algæ are to be found in the part of the lake investigated.

5. At least five varieties—possibly species—of bacteria have adapted themselves to the severe conditions in the lake.

In conclusion, I wish to heartily thank Professor C. T. Vorhies for the suggestions he has given me in the preparation of this paper.

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NOTES AND LITERATURE

BIOMETRIC STUDIES ON THE SOMATIC AND GENETIC PHYSIOLOGY OF THE SUGAR BEET

THE beet sugar industry, amounting to hundreds of millions of dollars every year, is the direct result of scientific breeding.

A biologist is loath to demur at any statement which attaches economic importance to scientific work of the kind in which he is interested. The statement may be true. Certainly no one can deny that far greater system and standardization of routine has obtained in the beet sugar industry than in many other branches of agriculture. But the trained scientific man who conscientiously works through some thousands of pages of the literature of sugar beet breeding and cultivation must hesitate before regarding it as a triumph of scientific method. He will rather, I think, feel that science has fallen woefully short of its possibilities in dealing with many problems of great theoretical interest and economic significance.

In no field of agricultural work is the failure of scientific and practical men to cooperate less excusable than in that of sugar-beet breeding. In the routine operations of sugar-beet production chemical data of a relatively satisfactory degree of trustworthiness are obtained for great numbers of individuals. It is not unconservative to say that millions of individual weighings, polarizations or analyses of various degrees of completeness have been made. For two decades the biometric formulæ which might have given meaning to some of these masses of data have been available. Yet the problems which might have been solved have remained unelucidated, to the material loss of both biology and industry.

It seems worth while to illustrate the truth of these statements by some of the advances in our knowledge of the genetic and somatic physiology of the sugar beet which have been made possible by the application of the biometric formulæ.

Consider first of all one of the simplest problems—that of the relationship between the weight of the root and the sugar content of its juice. Notwithstanding considerable discussion this

very simple problem was not definitely solved until 1913 when actual correlations[1] were available. Coefficients ranging from —.224 to —.756 for the relationship between weight of root and sugar content of juice in various short series of data were found. The results were published only after failure in a conscientious and systematic effort to obtain from the agricultural experiment stations really adequate series of data for detailed biometric analysis.

Fortunately the conclusions have since been fully confirmed. Pritchard,[2] in dealing with samples of 250 to 400 beets grown at Fairfield, Washington, found constants ranging from —.253 to —.499. Working with larger samples ($n = 3.784$) from Brookings, S. D., he found $r = -.258$, while Harris and Hogensen,[3] who had a sample of nearly 7,000 beets[4] from Utah cultures, found $r = -.288$.

The splendid work of these investigators leaves no doubt that the percentage sugar content decreases, and, as Harris and Gortner indicated on their limited series of data, in a sensibly linear manner, with increase in weight of root.

These studies, based as they are in some of these series, at least, upon closely bred material, fully justify the criticisms of the conclusions of Andrlik, Bartoš and Urban[5] by Harris and Gortner.[6]

Harris and Gortner have also found negative correlations between weight of root and total solids and coefficient of purity. Thus the larger roots have a smaller quantity of total solids, a lower percentage sugar content and a lower coefficient of purity.

[1] Harris, J. Arthur, and R. A. Gortner, "On the Relationship between the Weight of the Sugar Beet and the Composition of its Juice," *Jour. Ind. and Eng. Chem.*, 5, March, 1913.

[2] Pritchard, F. J., "Correlations between Morphological Characters and the Saccharine Content of Sugar Beets," *Amer. Jour. Bot.*, 3: 361–376, 1916.

[3] Harris, F. S., and J. C. Hogensen, "Some Correlations in Sugar Beets," *Genetics*, 1: 334–347, 1916.

[4] Unfortunately the constant is not altogether trustworthy because the largest and the smallest roots were excluded.

[5] Andrlik, K., V. Bartoš and J. Urban, "Über die Variabilität des Gewichtes und des Zuckergehaltes der Zuckerrübenwurzeln, und über die gegenseitigen Beziehungen dieser beiden Merkmale," *Zeitschr. f. Zuckerindustrie in Böhmen*, 36: 193, 1912.

[6] Harris, J. Arthur, and R. A. Gortner, "Further Notes on the Relationship between the Weight of the Sugar Beet and the Composition of its Juice," *Biochem. Bull.*, 2: 524–529, 1913.

That large roots yield an actually larger amount of sugar is to be expected, and Pritchard's coefficient for the correlations between weight of root and total sugar content is high.

Such results are obviously of great practical significance. Laying aside the possible desirability of modifying planting or cultivation in such a manner as to influence root size, the question of the selection of roots for sampling is one of real importance.

Much of the early American work on the sugar beet was devoted to determining where the crop will give a yield per acre and a sugar content and coefficient of purity satisfactory for economic work. Roots were sent by farmers to the Agricultural Experiment Stations, analyzed, and the results published in a great series of bulletins. But since size and percentage of sugar are correlated, and selection for size in the submitting of samples was rarely guarded against, the great mass of figures have little significance as measures of the merit of the cultures from which the samples were drawn.

If physical characters of the root be associated with sugar content or with purity of the juice, which is technically a highly important factor, physical characters may serve as a guide to selection.

Pritchard has devoted great care to the problem of the correlation between a number of the morphological features of the root and leaf and sugar content, and has determined the average percentage of sugar and average sugar content in synthetic types, *i. e.*, those embodying the most desirable of the morphological characteristics. The results are of technical rather than of general biological interest. The conceptions of a synthetic type—a conception that has already been emphasized in a quite different way by Raymond Pearl[7]—is well worth careful consideration by all those who have to do with breeding problems.

Both Pritchard[8] and Harris and Hogensen have extended their studies of the correlation of characters in the root to that of the interrelationship of the characters of the root and those of the fruiting shoots.

[7] Pearl, R., and F. M. Surface, "Selection Index Numbers and their Use in Breeding," AMER. NAT., **43**: 385–400, 1909. Also, R. Pearl, "Further Notes Regarding Selection Index Numbers," AMER. NAT., **46**: 302–307, 1912.

[8] Pritchard, F. J., "Some Recent Investigations in Sugar Beet Breeding," *Bot. Gaz.*, **62**: 425–465, 1916.

They agree that there is no correlation between the sugar content of a beet and the quantity of seed which is produced, but Harris and Hogensen find a correlation of $.308 \pm .013$ for the relationship between the weight of the seed beet planted and the weight of seed produced, whereas Pritchard, from a number of determinations, concludes that for beets of ordinary size such as are grown for factory use the correlation between root weight, percentage of sugar in roots and quantity of sugar in the seed root on the one hand and the number of grams of seed produced by the seed root is sensibly zero.

Harris and Hogensen find a correlation of about $+.399$ between height of plant and amount of seed produced, about $+.277$ between number of stems and weight of seed produced, and about $+.122$ between number of leaves and weight of seed produced.

Pritchard has shown that there is no correlation between the amount of seed which a beet root yields and the sugar content of its progeny. "The application of this fact to sugar breeding," says Pritchard, "is obvious, as extensive selection may be made for freer seed production without danger of sugar deterioration. Moreover, it affords an opportunity to reverse the order of selection by making the chief elimination in the seed generation and thus greatly reduce the amount of chemical work and increase the effectiveness of the working funds."

The physiological character *time required for maturing seed* has received some attention by Harris and Hogensen, who find a greater height and a higher production of seed in beets requiring a longer period for maturity. The coefficients are, however, low, $r = +.175 \pm .016$ for height and days required for maturing seed and $r = +.195 \pm .016$ for days required for maturity and quantity of seed produced. The correlation between the percentage of sugar in the mother beet and the number of days required for maturing seed is negative, $r = -.129 \pm .014$, *i. e.*, the beets with higher sugar content mature their seed more rapidly.

All these coefficients are very low. The experienced statistician will be cautious in regarding them as significant, remembering that when constants reach minimum values probable errors can not be given their normal weight. Those who have had personal experience in the biological phases of such work will realize its difficulties, and allow the questions of the significance of these correlations to remain open until more extensive

data are available. There are, furthermore, internal evidences of serious heterogeneity in the materials upon which these constants are based. Such irregularities as those seen in the frequency distributions of number of days required for maturing require explanation before coefficients based upon them can be given much weight.

The result of Pritchard's experiments which will arouse the widest interest is the conclusion that with due regard to the probable errors of random sampling, there is no correlation between the weight of the mother roots and the average weight, the average percentage sugar content or the average total sugar content of the progeny roots, that there is no correlation between the percentage of sugar in the mother beets and the average percentage of sugar in their progeny, between the actual amount of sugar in the mother beets and the actual amount of sugar in the progeny roots.

Thus in dealing with our long selected varieties of sugar beets the author is faced to the conclusion:

> Differences in the size and sugar content of individual beet roots show no evidence of inheritance. They are fluctuations, therefore, and apparently play no part in beet improvement.

The practical consequences of such a conclusion should be self evident. One European firm is said to carry out 300,000 analyses annually in the selection of roots for seed production. If the conclusion reached by Pritchard be of final significance, it justifies the assertion that "the cost of analyzing mother beets is an absolute waste of money."

Space precludes a discussion of the data given by Pritchard on the average composition of progeny rows and on the influence of environmental factors in observing genetic differences. From this side his paper must be read, and will later be reviewed in connection with one on the technical features of progeny tests.[9]

His studies show how small are the real genetic differences which may appear, how deeply these differences may be buried under those due to environmental factors, and how difficult in consequence must be the attainment of real progress in the further improvement of so highly selected an agricultural plant as the sugar beet.

[9] Pritchard, F. T., "The Use of Checks and Repeated Plantings in Variety Tests," *Jour. Amer. Soc. Agron.*, **8**: 65–81, 1916.

Pritchard is a mutationist rather than a selectionist.

The selection of choice roots by chemical and physical means has probably played no part in sugar beet improvement except where an occasional root has mutated and thus given rise to a superior physiological species.

One does not need to agree with the form of Pritchard's conclusion to recognize the great value of such studies as those which he has carried out. Full knowledge of the difficulties surrounding a task is one of the essentials to its accomplishment. When all the variables that enter into the problem of sugar-beet production and sugar-beet breeding are known in quantitative terms, it will be possible for the practical man to decide on the basis of the cost of labor and other economic considerations what operations can be dispensed with and what other changes in routine can be profitably made. Operations can then be more properly designated *scientific*.

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